

ACTIVATION OF HIBERNATING *COCCINELLA SEPTEMPUNCTATA* (COLEOPTERA) AND *PERILITUS COCCINELLAE* (HYMENOPTERA) AND THE PHOTOPERIODIC RESPONSE AFTER DIAPAUSE¹⁾

by

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To measure the progress of diapause termination in December and March and the difference in diapause intensity between populations from two altitudes, *Coccinella septempunctata* adults were exposed to 25° and to photoperiods 18L:6D or 12L:12D and the oviposition was recorded.

In early December, *C. septempunctata* females from 600 m had the pre-oviposition period 1/3—2/3 shorter than the population from 1500 m. It was shorter under long day and in injured coccinellids under short day than in intact insects under short day. In mid-March the pre-oviposition period was considerably shorter, both after the hibernation outdoors and under 15°, indicating thus that diapause was over in almost all females. Photoperiodic response in post-diapause insects was shown by a gradual halt of oviposition after a decrease in daylength.

In contrast to pre-oviposition of *C. septempunctata*, the pre-pupal period of *Perilitus coccinellae* did not get shorter between December and March.

Whereas detailed studies (review in Hodek, 1973) have been devoted to the induction of diapause in *Coccinella septempunctata*, only preliminary experiments have been conducted on its termination (Bonnemaison, 1964, Hodek, 1962, 1970) and nothing has been known about the prerequisites for post-diapause development. We now report on the activation in December and March by warm temperature and long day or injury, progress of the final phase of diapause both outdoors and in the laboratory 15°, difference between populations from two altitudes and photoperiodic response of post-diapause reproducing females.

MATERIAL AND METHODS

The coccinellids were collected near Digne (Basses Alpes, France, ca. 44° northern latitude). High altitude samples were collected from under *Buxus* bushes on the peak of Mt. Cousson (1512 m), other samples were from a hill (about 600 m) close to Digne. The samples were taken on 2 December 1972 and 20 March 1973. The coccinellids from Cousson were heavily parasitized by *Perilitus coccinellae* (Hymenoptera, Braconidae).

¹⁾ Dedicated to Prof. Dr. Jan de Wilde, Wageningen, on the occasion of his 60th birthday.

Part of the sample of 2 December was stored at $15^{\circ} \pm 2^{\circ}$ in darkness till the beginning of the second experiment on 20 March. Activation was performed at $25^{\circ} \pm 1^{\circ}$ and long day (18 L:6D) or short day (12 L:12 D). To compensate for the weaker radiation energy, the temperature was kept 0.5° — 1° higher under short day.

The beetles were injured by cutting off the second pair of wings of both sexes. Single pairs of coccinellids were kept in plastic transparent containers (10 cm diam.) with air-permeable lids. The coccinellids were supplied daily (exceptionally every other day) with a surplus of aphids (*Acyrtosiphon pisum*), reared under long day. Pre-oviposition longer than 2 weeks has been considered as an indication of diapause.

RESULTS

Activation in the middle of the hibernation period

Beetles from the Cousson and Digne populations were exposed to long-day or to short-day conditions in early December. In one short-day series the beetles were injured (Table I).

Long-day activation

In long-day conditions all females began to oviposit. The pre-oviposition period of the females from Digne was on average 12.3 days, with a median of 10 days. Only three Cousson females were not parasitized and oviposited after 13, 17 and 32 days. Although the average of these three data — 20.7 days — has a low statistical value, it indicates that — similarly to the results from other conditions — the sample from Cousson is slightly more resistant to activation.

The oviposition rate was high, at least in the Digne sample (Fig. 1). During the first 2 weeks it averaged nearly 50 eggs per female per day and it rarely decreased to less than 40 eggs. Even the minimal values were not very low, amounting usually to over 20 eggs.

The Cousson females oviposited less, but the peak of their reproductive activity — which was attained 2-3 weeks later — was comparable to the oviposition rate of the females from Digne. The post-oviposition period was short in both samples (Table I).

Activation of intact beetles under short day

All healthy, nonparasitized females oviposited with the exception of one female from Cousson which died after 43 days without having laid eggs. The activation was much slower than under long day: in females from Digne the pre-oviposition period averaged 20.0 days (Table I). Due to heavy parasitization by *P. coccinellae* only three females from Cousson oviposited, and the pre-oviposition period was 11, 27 and 34 days. This indicates, similarly to long-day conditions, a weaker activation of the Cousson females.

The females deposited less than half of the number of eggs laid by long-day

TABLE I
Reproductive activity of Coccinella septempunctata females transferred in early December from the open to 25°

Photoperiod	Locality	18 L.: 6 D				12 L.: 12 D					
		Digne aver. (range)	med. n	Cousson aver. (range)	med. n	Digne aver. (range)	med. n	Cousson aver. (range)	med. n		
Pre-oviposition period (days)	intact	12.3 (9—23)	10	20.7 (13—32)	17	3	20.0 (9—45)	13	24.0 (11—34)	27	3
	injured						13.3 (9—21)	13 ¹⁾			
Rate of oviposition in days 25—34 (eggs/female/ day)	intact	54.7 (37—81)	8	27.6 (3—54)	3	3	25.5 (11—44)	6	35.3 (28—43)		3
	injured						26.0 (19—40)	7	15.3 (1—48)		7
Fecundity (eggs/female)	intact	2134 (705—4615)	9	1576 (1227—2058)	3	3	896 (392—1834)	8	688 (262—1217)		3
Post-oviposition period (days)	intact	4.3 (1—15)	4	6.5 (6; 7)	6.5	2	2.9 (1—5)	2.5	2.0 (1—4)		3

¹⁾ Mean data for the above sample if two females with extremely long pre-oviposition period were excluded

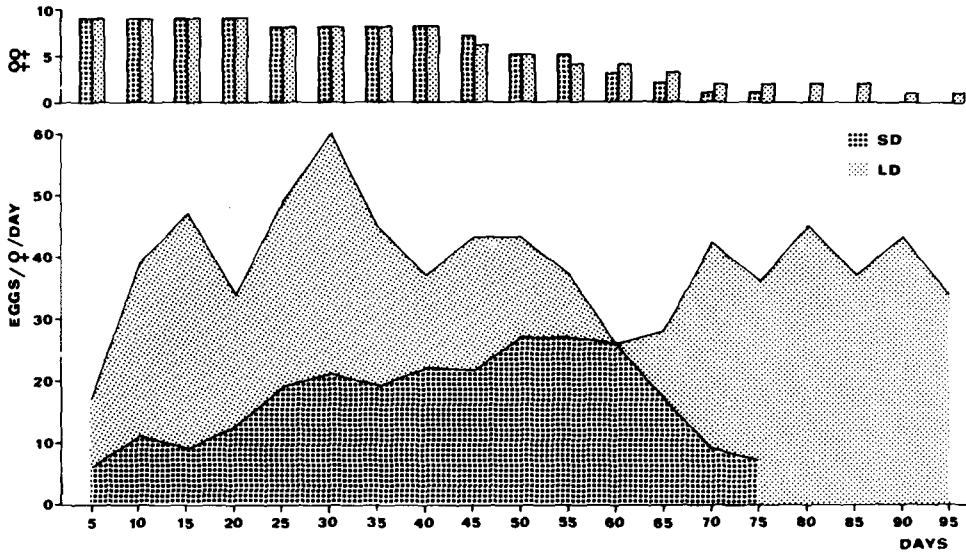


Fig. 1. Daily averages of oviposition in *Coccinella septempunctata* females transferred in December from outdoors to 25° and long (shaded) or short day (dark-shaded). Above — number of live females; (all females oviposited); below — 5 days' averages of daily oviposition. (After day 55 the average oviposition is less reliable as the number of females is reduced to three or less.)

females (Table I). However, the oviposition rate of Digne females did not decrease until the 60th day (Fig. 1) and the post-oviposition period was short. This is in contrast with the three females from Cousson in which the oviposition rate decreased substantially — to about one fifth — 6 weeks after the transfer.

Activation of injured beetles under short day

With the exception of one female from Cousson, all injured coccinellids oviposited. The pre-oviposition period of Digne females was about the same as in intact beetles under long-day conditions. Whereas the average of 11.3 days was one day lower, the median of 12 days was 2 days higher (Table I). The females from Cousson began ovipositing later. The difference between the two populations had the same trend as in the other two experimental conditions.

Although injury hastened the onset of oviposition in the Digne females, it did not increase their oviposition rate. The Digne females had about the same rate of egg laying under short day, whether or not injured (Table I). The rate of oviposition was considerably lower in the Cousson females.

Activation after hibernation

Coccinellids sampled on Mt. Cousson ("outdoor") in late March were compared with the beetles collected from the same hibernation quarters in early December and then stored in darkness at 15° ("stored"). Both series were exposed simultaneously to 25° and long day.

In both series almost all females were activated (85% and 89%). In most females also the pre-oviposition period was similar in both series: without the two extremes of 69 and 75 days, the data for "outdoor" females (aver. 11.5, med. 11, min. 7, max. 27 days) would have been nearly identical with those of "stored" females (aver. 12.2 days, med. 10, min. 8, max. 24 days). When included, the two extremes increased the average of "outdoor" coccinellids (Table II).

The rate of oviposition was estimated in two ways. One value was obtained for the first 25 days, as some of the beetles were used later for another experiment. The other value gives the mean oviposition rate for the entire life of females which died under unchanged experimental conditions. In both ways the reproductive activity amounted to about one egg batch per 2 days in both series.

Although "stored" females have slightly better parameters of activation than the "outdoor" females (Table II) the difference is not significant.

TABLE II

Reproductive activity of Coccinella septempunctata females transferred in March to 25° and long day¹⁾

	Incidence of non-reproductive females		Pre-oviposition period (days)			Rate of oviposition (batches/female/day)			
	%	n				during first 25 days		during whole life	
			aver. (range)	med.	n	aver.	n	aver.	n
"outdoor" females ²⁾ (without 2 extreme values)	14.8	27	17.1 (7—75) 11.5 (7—27)	13	23	0.45	10	0.47	10
"stored" females ³⁾	10.7	28	12.2 (8—24)	10	25	0.54	17	0.62	6

¹⁾ The beetles were sampled on Cousson (1512 m) and fed with *Acyrtosiphon pisum*;

²⁾ Sampled on 20 March;

³⁾ Sampled on 2 December, stored for 14 weeks at 15° const. darkness.

Response of ovipositing females to photoperiod

After hibernation and 40 days of activation at 25° and long day some of the females ("outdoor" and "stored") were transferred to short day at the same temperature. The beetles responded quite soon to the decrease in photophase (Fig. 2). The rate of oviposition decreased after 55 days of experiment (i.e., 15 days after transfer). After 70 days most of the females stopped egg production and the average oviposition of the remaining females was very low. After 75 days (i.e., after about one month spent under short day) no female continued egg laying. Oviposition period lasted only 18.4 (4—28) days. In contrast, fecundity of the females kept under long day, increased for 30 days of experiment and remained

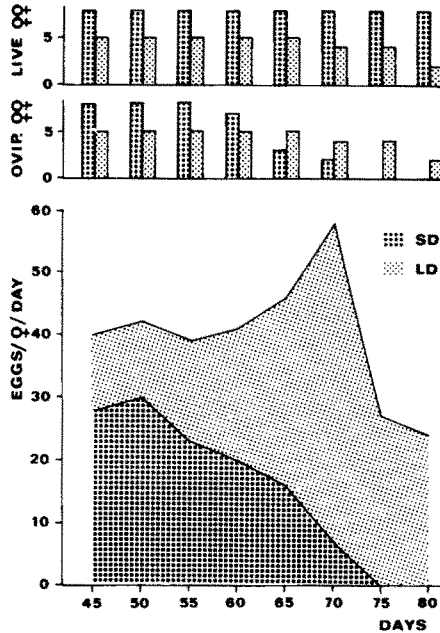


Fig. 2. Photoperiodic response of activated *Coccinella septempunctata* females as indicated by oviposition intensity. After 40 days under long day part of females was transferred to short day (dark-shaded), while controls were kept under continuous long day (shaded).

quite high until their death. Duration of the oviposition period under continuous long day (aver. 42.0 days, with min. 26, max. 54 days) was thus more than twice as long as in the females transferred to short day.

The response to the decrease of photoperiod is also shown by the duration of post-oviposition periods. Whereas the control females left under long day oviposited almost till their death and their average post-oviposition period was thus only 2.4 (2—3) days, the short-day females stopped oviposition long before their death. The established duration of their post-oviposition period (aver. 31.0 days, min. 10, max. 51 days) does not give a good evidence of longevity, as five of eight females were still living 55 days after the transfer, when the experiment was discontinued. We may assume that the longevity might have considerably surpassed this period, as the decrease in daylength evidently re-induced dormancy.

Pre-pupal development of Perilitus coccinellae

The larvae of *P. coccinellae* normally complete their development in spring early in the active life of their host (Hodek, 1973). When the beetles were activated by transfer to the laboratory, the dormancy of the parasite larvae was also terminated, they completed their development and pupated in cocoons between the legs of the beetles.

The duration of the pre-pupal period of *P. coccinellae* was recorded as a period

TABLE III

Pre-pupal development of Perilitus coccinellae larvae in activated coccinellids

sample (date)	Origin and treatment of coccinellids		Duration of development (days)					
	locality	conditions	in host females			in host males		
			aver. (range)	med.	n	aver. (range)	med.	n
early Dec.	Cousson	long day	12.8 (12—14)	12.5	6	13.1 (12—19)	12	6
	Digne	long day	—	—	0	15.5 (13—19)	15	4
	Cousson	short day injured beetles	—	—	0	12.5 (12—14)	12	4
	Digne	short day injured beetles	—	—	0	13.0 (12—14)	13	3
	Cousson	short day intact beetles	15.2 (12—19)	15	4	14.5 (12—21)	13.5	6
	Digne	short day intact beetles	—	—	0	—	—	0
early Dec.	Cousson	long day (after 14 weeks storage at 15° in dark)	11.9 (8—18)	11.5	12	11.0 (9—12)	11	8
late March	Cousson	long day	12.6 (9—18)	12	16	11.0 (9—17)	11	21

between the transfer to the laboratory and the formation of the cocoon. It did not seem to be influenced by the sex of the host and was affected by the experimental conditions usually in the same way as the pre-oviposition period of the coccinellid (Table III).

In the first sample, transferred from Cousson to the laboratory in early December, the pre-pupal period was slightly longer (av. 15 days) in short-day intact coccinellids than in short-day injured beetles or under long day (av. 13 days). The pre-pupal period remained unshortened, lasting on the average 11—13 days under long day in both samples activated 14 weeks later. No difference was found between the “stored” and “outdoor” sample.

DISCUSSION

Activation

In early December, about two thirds of females of the “low-altitude” sample had a short pre-oviposition period indicating post-diapause development. In the “high-altitude” population still most females were in diapause. In this population diapause was apparently terminated in almost all females before late March both in the open and in the cooled room. This was indicated by a short oviposition delay after the transfer to the laboratory (Table II), as compared with the value for the same population in December.

Storage of insects at 15° between December and March was not inferior to hibernation outdoors as far as the subsequent reproduction is concerned (Table

II). Although the stored beetles may have experienced some chilling in the open in November, long exposure to positive temperatures near 0° appears not to be a prerequisite for successful hibernation of *C. septempunctata*, at least in south-eastern France.

Response to shortening photophase

Ovipositing females transferred from long to short day responded by a steep decrease in oviposition rate and later by a complete arrest of oviposition (Fig. 2). This demonstrates that a photoperiodic response can occur in *C. septempunctata* soon after the end of diapause. This phenomenon, found for the first time in *Aelia acuminata* (Hodek, 1971, 1977) might be more common in insects with adult diapause. It was shown also in the grasshopper *Oedipoda miniata* (Pener & Broza, 1971).

We used the stationary photoperiod to get a pronounced short-day response. We assume, however, that in spring under natural conditions the increasing intermediate photophase of about 14–15 hr would allow the coccinellids to oviposit longer. In some insects, the effect of changing daylength on activation of dormant adults has been established e.g., in *Galeruca tanacetii* by Siew (1966), in *Chrysopa carnea* by Tauber & Tauber (1970) and in *Chilocorus bipustulatus* by Zaslavsky (1973).

There is an apparent discrepancy between two responses of *C. septempunctata* females to the same stationary short daylength. The sample from early December oviposited under short day, although after a longer delay and less intensively than under long day, and oviposition lasted until death. The one-third shorter photophase apparently decreased the overall activity, including food intake and egg production. Short day, however, did not reinduce diapause. By contrast, in the sample of March, activated for 40 days under long day, the substantial decrease in daylength did induce diapause. Reproduction stopped and the post-oviposition period lasted long.

Two important differences underlie the contrasting response of the dormant and activated insects. Dormant females transferred in early December from outdoors to laboratory short-day conditions, experienced strong positive signals: increase in temperature and light intensity, and presence of suitable food. Even the stationary short photophase of 12 hr represented an improvement compared to the shortening of photophase from 9 hr to 8.5 hr in the open. In the sample from March, however, the females experienced a strong negative signal consisting of a steep decrease in photophase by 6 hr and no positive stimuli, the other environmental factors remaining unchanged.

The second difference consists in the contrasting physiological states of the experimental females. Dormant insects are specifically responsive to the proper signals for activation. On the other hand, the responsiveness to signals inducing dormancy is essential for reproducing females, as it enables them to hibernate a second time.

Experimental analysis of diapause in *C. septempunctata* both in southern France

and central Bohemia (Hodek & Růžička, *in prep.*) showed a similarity in principal traits with diapause of *A. acuminata* (Hodek, 1977): (1) the intensity of diapause gradually diminishes in the course of autumn and winter; (2) diapause ending processes have a wide temperature range — they can proceed at 15° and even 25°; (3) the photoperiodic responsiveness disappears with diapause termination, but (4) it is regained with the resumption of reproductive activity.

Regulation of reproductive activity in insects with adult diapause

Our results on *C. septempunctata*, particularly the similarity between the effect of injury and long day, corroborate our concepts of adult diapause based mainly on the study of *A. acuminata*.

We have found in that species that environmental factors may be mutually compensated in producing the same effect (Hodek, 1977, and earlier papers). There is abundant evidence for this interrelationship also from many other species, e.g., a low photoperiodic stimulation may be compensated by a strong stimulation by temperature, or an intensive stimulation by photoperiod may be invalidated by unsuitable food (De Wilde & Ferket, 1967). The reproductive activity can be modified also by changes in intensity of illumination (Krehan, 1970) or by population density (Stross, 1969). The most complex theory explaining the dependence of various types of photoperiodic responses on temperature is based on experiments with *Chilocorus bipustulatus* (Zaslavsky, 1973).

While the primary role of the brain in the control of diapause via corpora allata was well-demonstrated both as regards the absence of stimulation (in *Leptinotarsa decemlineata* — De Wilde & De Boer, 1969, De Wilde & Schipholt, 1974; in *Anacridium aegyptium* — Girardie & Granier, 1973) and as regards the inhibition (in *Pyrrhocoris apterus* — Hodková, 1977), it has still remained obscure how the different signals from the environment and from the insect body are computed. We suppose that the message for the target organs (endocrine system, gonads) is processed in a co-ordination centre of the brain. In her neuroendocrine integration concept B. Scharrer (1967) assumes that the processing of stimuli takes place in the neurosecretory neurons. At least four kinds of information should be handled in the co-ordination centre: (1) environmental signals (of photoperiod, temperature, food quality, population density, etc.); (2) information on the state of the insect body (possibly changed by mechanical injury, disease, insecticides, etc.); (3) messages from the interval timer measuring the duration of activity or inactivity; (4) feed-back messages on the activity or inactivity of target organs. The centre should be combined or in close relation with “memory link” (Goryshin & Tyshchenko, 1974) where the information is accumulated and stored.

The complex environmental message (eM) is thus modified according to the information above, 2-4. In an insect with advanced diapause or in an injured insect a weak eM can therefore produce an effect similar to a strong eM at the onset of diapause in an intact insect. Wounding has already been reported in several insects as diapause terminating stimulus. The activation by injury is supposed to be indirect, via sensoric pathways affecting the neuroendocrine system (Cassier,

1967) or direct, due to fundamental changes in metabolism (Rohdendorf & De Wilde, 1972).

Difference between the populations from two altitudes

Coccinellids collected on Mt. Cousson (1512 m) had a longer pre-oviposition period than the population from 600 m. This is not surprising as *C. septempunctata* displays a large variability in diapause traits (Hodek, 1973). Although not migrating obligatorily to the mountains (like *Hippodamia convergens* or *Semiadalia undecimnotata*) *C. septempunctata* prefers to use higher areas as hibernation sites. As the displacement to hibernation quarters is stepwise, we may suppose that the individuals with the earliest diapause onset occupy places situated at highest altitudes. In this part of population the proportion of the obligatory onset of diapause is very important and thus the average diapause intensity is high.

Activation of Perilitus coccinellae

Mellini (1975) assumes a direct dependence of the development of parasites on the presence of cerebral and/or gonadotropic hormones of the adult host. This is in concert with the similar differences in the pre-pupal period of the parasite and the pre-oviposition period of the host found under various activation treatment of the sample from December (Table III). The fact that the pre-pupal period was not shortened between December and March (in contrast to the pre-oviposition period of the host) may indicate either independence from the host or more likely a complex dependence both on the host's hormonal level and the environmental stimuli.

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RÉSUMÉ

ACTIVATION DE COCCINELLA SEPTEMPUNCTATA ET DE SON PARASITE PERILITUS COCCINELLAE (HYMÉNOPTÈRE), EN DIAPAUSE HIVERNALE; RÉPONSE AUX CONDITIONS DE PHOTOPÉRIODE APRÈS DIAPAUSE

En vue d'apprécier l'intensité de la diapause et son état d'avancement au cours du temps, en fonction des conditions d'hivernage, deux populations de *Coccinella septempunctata* sont récoltées dans le sud-ouest de la France, l'une à 600 m d'altitude, l'autre à 1512 m. Les insectes sont prélevés, d'une part, au milieu de la période d'hivernation (2 décembre), d'autre part, en fin de cette période (20 mars). Ils sont soumis à des photopériodes longues (18 L:6D) ou courtes (12 L:12D), dans des conditions de température de 25°, et on compare le délai nécessaire pour obtenir la ponte (période de pré-oviposition). Certains lots ont subi une mutilation, à titre expérimental: section des ailes postérieures.

Chez les insectes prélevés début décembre, la durée de la période de pré-oviposition est de 1/3 à 2/3 plus courte pour la population de plaine hivernant à 600 m d'altitude. L'activation est plus rapide en jours longs (18h de photophase); elle est aussi plus rapide chez les coccinelles mutilées que chez des femelles indemnes, lorsqu'elles sont placées en jours courts.

Chez les insectes prélevés en mi-mars la période de pré-oviposition est beaucoup plus courte; il en est de même chez des insectes prélevés en décembre mais maintenu en hibernation artificielle au laboratoire à une température de 15° et à l'obscurité. Des femelles réactivées en jours longs se révèlent sensibles dès l'achèvement de la diapause à une réduction de la photopériode qui provoque un arrêt progressif de la ponte.

En contraste avec les variations observées dans la durée de la période de pré-oviposition chez les coccinelles réactivées en décembre ou en mars, la période de pré-émergence de leur parasite *Perilitus* reste la même et n'est pas plus courte en mars qu'en décembre.

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