A Field Study of Diapause in *Coccinella novemnotata* (Coleoptera: Coccinellidae)[1,2]

R. D. McMullen

Research Station, Canada Department of Agriculture,
Summerland, British Columbia

Abstract

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There are two generations of *Coccinella novemnotata* Herbst per year in central California. The adults of the spring generation aestivate and those of the fall generation hibernate. A field study of the physical and biological factors possibly influencing induction of diapause in the adult was conducted. All stages of the spring generation are subject to a regime of long, increasing photoperiods and increasing mean temperatures, while all stages of the fall generation are subject to a regime of short, decreasing photoperiods and decreasing mean temperatures. In non-irrigated areas with native vegetation the reproductive cycle of this species is synchronized with the availability of prey species. In irrigated agricultural areas prey species are relatively abundant throughout the summer but the adults of the spring generation still aestivate. It is hypothesized that diapause is induced in the adult by both short and long photoperiods and that intermediate photoperiods are required for reproduction.

The biology of *C. novemnotata* is described briefly with emphasis on the aggregational behavior of the adult.

Introduction

Coccinella novemnotata Herbst is bivoltine in the San Joaquin Valley of California. One generation is produced in the spring and one in the autumn. The adults of the spring generation undergo an aestival diapause and the adults of the fall generation undergo a hibernal diapause. Little attention has been paid to diapause in *C. novemnotata*, the only report in literature being that of Hagen (1962), which established the occurrence of an imaginal diapause state in each of the generations. The scope of this paper is the description of the biology of *C. novemnotata* in the field, with particular emphasis on the appraisal of environmental factors influencing the induction of diapause.

Methods

Observations on the biology and behavior of *C. novemnotata* were conducted from September 1961 to September 1962 in irrigated alfalfa, lucerne and barley fields and in surrounding uncultivated lands near Dos Palos, California. Samples to determine the relative population densities of *C. novemnotata* and prey species were restricted to a single alfalfa field that in late 1961 contained a very heavy infestation of the pea aphid, *Macrosiphum pisi* (Harris). Beetle and aphid populations were sampled at varying intervals, the frequency depending upon the rate of change of the status of the beetle populations. When adult beetles were in diapause, samples were taken once or twice a month. When adult beetles were reproducing, or when the beetle population consisted of immature stages and recently emerged adults, samples were taken once or twice a week.

The sampling procedure was varied according to the situation in the field. Generally 50–100 sweeps were made with a 13-inch insect sweep net to sample the active stages of the beetles. Observations on inactive stages, eggs, pupae and dormant adults, were made by parting the foliage of the plants with the handle of a sweep net. When diapausing adults were forming into aggregations the numbers of adults in randomly selected square-yard quadrats were counted.
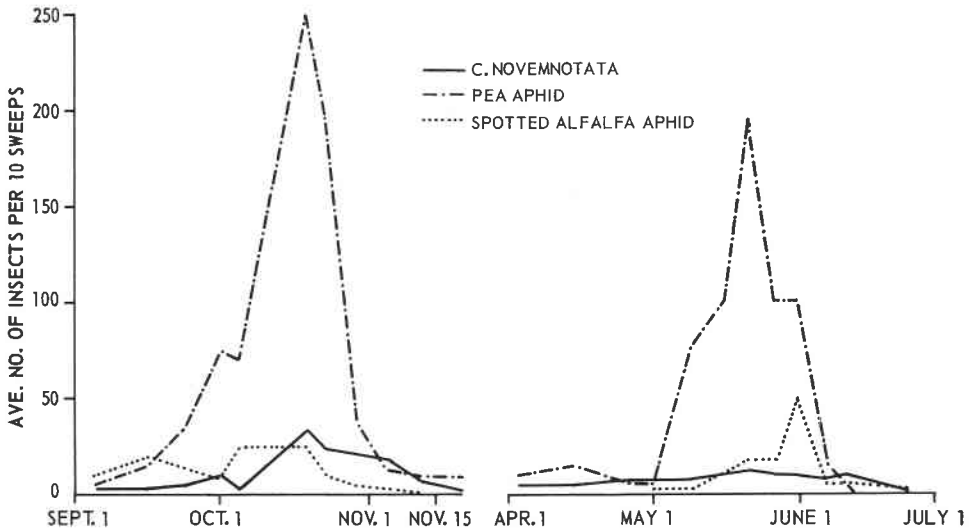
Fig. 1. Relative abundance of the actively feeding stages of *Coccinella novemnotata;* the pea aphid, *Macrosiphum pisi,* and the spotted alfalfa aphid, *Therioaphis maculata,* in alfalfa fields near Dos Palos, California.

Once located, aggregation sites were marked with identifying ribbons for additional observations.

Subsamples of adults collected in the field were dissected to determine the extent of body fat and gonad development and whether they had fed recently. To determine the intensity of diapause in naturally diapausing adults, samples of dormant beetles were collected at intervals from aggregations in the field and reared in the laboratory under conditions of temperature and photoperiod optimal for reproductive development.

Continuous records of temperature were obtained from a hygrothermograph housed in a standard United States Weather Bureau shelter situated in one of the alfalfa fields used in this study. Data for daily photoperiods at 37° N. latitude were obtained from the Smithsonian Meteorological Tables (Marvin and Kimball 1931).

Results and Discussion

The relative abundance of *Coccinella novemnotata* and its main prey species in alfalfa fields, *Macrosiphum pisi* and *Therioaphis maculata,* are shown in Fig. 1. The line indicating the relative abundance of *C. novemnotata* is based on the stages, larvae and non-diapausing adults, that actually feed on prey. The seasonal occurrence of the developmental stages, reproductive adults and diapausing adults of *C. novemnotata* are shown in Fig. 2.

Eggs

The eggs of *C. novemnotata,* which are bright orange and sausage-shaped, are laid in tight clusters, each egg set vertically and cemented to the substrate. The most common oviposition site observed was the undersurface of leaves, but occasionally eggs were also observed on stems and petioles. Of six occasions when female *C. novemnotata* were observed ovipositing in the field the smallest number of eggs laid in a single cluster was four and the greatest number was 16. Eggs were difficult to locate, particularly when gravid females were at low densities. The oviposition period for each generation may best be estimated as the interval
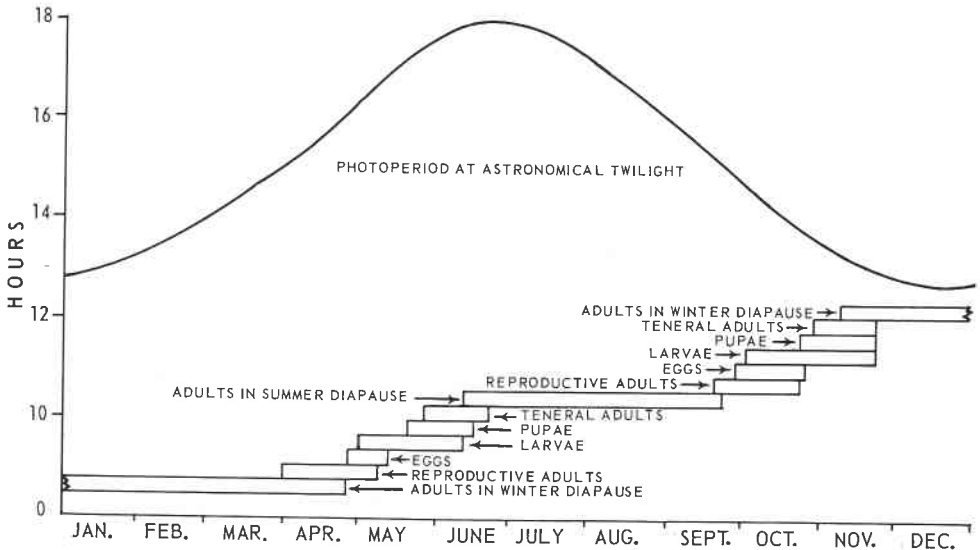
Fig. 2. Seasonal occurrence of the immature stages, teneral adults, adults in diapause and reproductive adults of *Coccinella novemnotata* near Dos Palos, California, in respect to photoperiod.

between the dates on which the first and last gravid females were captured. In the fall of 1961, eggs were probably present from 22 September to 23 October, a period of 32 days. In the spring of 1962 the probable oviposition period was from 26 April to 8 May, a period of 13 days.

Larvae

There are four instars in the larval development of *C. novemnotata*. All stages actively search for prey and are voracious feeders. Larvae searching for prey move randomly over all parts of the plants. They travel rapidly while searching and only sense the presence of prey when they contact them with their heads. Presence of prey did not appear to be sensed either by sight or by contact with the legs or body parts.

The first larvae of the fall generation in 1961 were captured on 4 October. It is quite probable that a few larvae were present one week earlier because the first larvae captured were second-instar larvae and, also, gravid females were collected 13 days earlier. The greatest number of larvae were collected on 18 October when 340 larvae per 100 sweeps were taken. Living larvae were collected in sweep samples until 20 November. Most of the larvae present at this time probably failed to mature because none of the larvae developed to maturity when reared in the laboratory. Probably they were severely injured by freezing temperatures that occurred on several nights during the previous week. In 1962 larvae of the spring generation were found in samples from 1 May to 11 June. The peak of the larval population occurred around 25 May when an average of 28 larvae per 100 sweeps was recorded.

Pupae

Just prior to molting to the pupal stage the fourth-instar larva cements its posterior to a substrate, usually a leaf or stem, by means of a secretion from the anal glands. After the molt the larval exuvium shrinks to a small collar around the posterior of the pupa. The pupa clings to the larval exuvium, which remains

cemented to the substrate by means of strong hooked spines at its posterior. The pupal stage of *C. novemnotata* is of the complex, or incomplete, type. The appendages are enclosed within separate sheaths that adhere to the body. The abdomen is flexible and allows the pupa to make violent movements when it is disturbed.

The pupae of the spring generation were typically a bright salmon-orange color without black markings. Those of the fall generation were also basically salmon-orange but with the heavier sclerotized areas colored black. No particular kind of site appeared to be selected for pupation. Pupae were commonly found on the leaves and stems of alfalfa plants, on succulent and dry weeds and grasses and even on stones, sticks and fence posts.

In the fall of 1961 pupae were observed from 23 October to 22 December. It is unlikely, due to cold weather, that any pupae present on 20 November or later survived because none that were taken into the laboratory produced adults. Pupae of the spring generation were observed from 19 May to 11 June.

Adults

In the fall of 1961 the first teneral adults were collected on 27 October. "Teneral" refers to the stage of recently emerged adults when the integument is not fully hardened nor is completely colored. The integument hardens sufficiently within a few hours after emergence to enable the beetles to feed on aphids. Attainment of full coloration takes about two days, but this can vary with temperature. Although there was only a four-day period between the capture of the last gravid females and the appearance of the first teneral adults, and since no females were found subsequently with evidence of reabsorbed eggs in their ovarioles, it is presumed that none of the adults of the spring generation re-entered diapause to hibernate with their progeny. Following the collection of the first teneral adults in October 1961, and continuing to the spring of 1962, all of the adult females had immature ovaries lacking any evidence of ovogenesis. Non-teneral adult females almost always contained moderate to large amounts of fat body tissue.

In 1962 the earliest collection of recently emerged adults of the spring generation was made on 25 May, 17 days after the last individuals of the over-wintered fall generation were taken. As noted in the fall of 1961 no evidence was encountered to suggest that the overwintered adults re-entered diapause with their progeny. Subsequent to 25 May and up to 7 September all of the females had immature ovaries without any evidence of ovogenesis.

Adult Behavior

The behavior of adults prior to and during the formation of aggregations in the fall of 1961 and the early summer of 1962 was closely observed. Teneral adults began to feed soon after emergence from the pupa. Searching and feeding activities were continued for approximately seven to ten days, after which adults entering the diapause stage became quiescent and tended to rest in the shelter of any dense vegetation. Fat body development in recently emerged adults was slight, whereas in adults that had fed for several days and in adults in diapause the fat body tissues were greatly enlarged. The mid-guts of beetles that were feeding on aphids were distended, thin walled, semitransparent, and packed with green aphid parts. In contrast, the mid-guts of beetles that had attained the quiescent stage were reduced to a whitish, opaque, thick-walled tube that contained a brown fluid.

In the fall of 1961 first quiescent beetles occurred singly and in small groups in sites where vegetation afforded cover. Later they moved from locations with only sparse cover and congregated in large numbers, from 100 to several thousand, in sites where very dense matted vegetation afforded greater protection. In the fall of 1961 the alfalfa fields were in stubble and provided generally sparse cover. The majority of the large aggregations formed along the margins of the field beneath matted dry grasses and weeds. During the cold weather of December through February most of the adults in the aggregations worked their way into the topsoil and plant debris so that few beetles were visible on the surface.

In mid-June, 1962, the distribution of quiescent adults in alfalfa fields was random. By the end of June the distribution was distinctly colonial; small widely scattered aggregations of 10–30 adults had formed. At this time the alfalfa in the fields was 12–18 inches tall and the stands were generally uniform. A comparison of the height and density of the alfalfa at sites where aggregations were formed and at sites where no aggregations were formed did not reveal any apparent characteristic for which the aggregating adults might have shown preference. Also, by the end of June a few aggregations of 10–30 adults each were formed along the margins of the fields. In this case a marked preference was apparent for dense stands of green succulent broad-leaved weeds over relatively dry, although dense, stands of grasses.

In early July after the alfalfa had been cut and baled the aggregations of adults within the alfalfa fields were totally dispersed. Examination of previously marked aggregation sites along the field margins showed that the number of beetles in these sites had increased 10- to 25-fold, which suggested that the beetles disturbed by the harvesting had fled to these sites. Aggregations were most commonly associated with the following weeds: *Sonchus oleraceous* L., *S. asper* L., *Latuca scariola* L., *Rumex* spp. and *Plantago* spp. No aggregations were found associated with dry herbage or in dry wasteland surrounding or near any of the fields investigated.

Dispersal of adults from aggregation sites in both the spring and the fall was prolonged over a period of three to four weeks, although the majority of the beetles left the aggregations within a period of one week. On 5 September 1961, non-gravid females that had apparently left aggregations were found feeding on aphids in alfalfa fields. However, the peak dispersal from aggregations occurred during the week of 15–22 September. On 2 April 1962, it was estimated that 5 per cent of the aggregating adults had dispersed. The greatest rate of dispersal occurred between 26 April and 1 May. On 2 April most of the adults in the aggregations were torpid, moving about very little when disturbed. On 16 April they were easily excitable but very few flew when disturbed, and by 1 May the aggregations were completely dispersed.

Observations on the aggregating behavior of *C. novemnotata* suggested that among some species of Coccinellidae there is a tendency to form monospecific aggregations. In June 1962, when aggregations were located in alfalfa fields they consisted almost entirely of this species, although other species were present in the field. When harvesting operations forced the reformation of aggregations in other sites along the margins of the fields, the resulting aggregations were of mixed species, mainly *C. novemnotata, Hippodamia convergens* Guer., *H. quinque-fasciata punctulata* Lec. and *Paranemia vittigera* Mann. One week after this occurred it was apparent that the various species were moving about to reform nearly monospecific aggregations. This was particularly evident in the case of *C. novemnotata* and *P. vittigera*. A few adult *H. quinquefasciata punctulata* and

H. convergens were usually present with aggregations of *C. novemnotata* or *P. vittigera* but the latter two species were only rarely present in aggregations of *H. quinquefasciata punctulata*. *H. convergens* was not present in large enough numbers at any time to constitute what might be termed an aggregation.

From the evidence presented above it seems most likely that the conditions required by aestivating *C. novemnotata* for aggregation sites are dense shade and a moist microenvironment. The gathering into aggregations in such sites probably serves to reduce water loss during aestivation. The mechanical protection of dense plant cover reduces water loss by reducing direct solar radiation and air movement. Moisture provided by transpiration of green succulent plants can maintain a high atmospheric humidity thereby reducing water loss by surface evaporation and respiration. Because adults in diapause do not feed they have no way of replenishing water in body fluids except possibly by fat metabolism.

The cold, wet conditions to which hibernating aggregations of adult beetles are exposed are totally different from those to which the aestivating adults are exposed. A different explanation of benefits derived from the aggregational behavior of the two generations must be assumed, unless it is postulated that the behavior pattern advantageous to survival of the spring generation is repeated by the fall generation even though the mortality selection factor avoided by the behavior is absent. Typically, the aggregation sites selected by hibernating adults afforded mechanical protection of the same degree as sites chosen by aestivating adults. However, the vegetation was invariably dry, in comparison to that selected by the aestivating adults. Also the hibernating aggregation sites usually included a loose layer of plant debris into which the beetles burrowed. The main advantage offered by the typical winter aggregation site is protection from extreme variations of temperature.

Other than the apparent protection from environmental severities, it has been postulated (Chapman 1954; Edwards 1957) that the basis for aggregational behavior in coccinellids, as well as for other insects, is to ensure meeting of the sexes and fertilization. This might also be the case for *C. novemnotata*, particularly when population densities are very low. But in the circumstances under discussion the population densities were high and mating was frequently observed prior to, during and after the aggregations were formed.

A comparison of weekly mean temperatures and average photoperiods shows clearly that these factors were operating at different levels during the spring generation compared to the fall generation. Generally, the fall generation was subject to short photoperiods and decreasing temperatures, and the spring generation to long photoperiods and increasing temperatures. The lowest and highest mean weekly temperatures during each of the various stages of development in each generation were: eggs, 65° and 72° F. in the fall, and in the spring 56° and 68° F.; larvae, 51° and 68° F. in the fall, and 60° and 68° F. in the spring; pupae, 44° and 57° F. in the fall, and 60° and 75° F. in the spring; teneral adults, 44° and 57° F. in the fall, and 60° and 75° F. in the spring. Similarly the average photoperiods, calculated on the basis of the diurnal occurrence of astronomical twilight during the periods when the various stages of development of each generation were present, were: eggs, 14 hours 30 minutes in the fall, and 16 hours 30 minutes in the spring; larvae, 14 hours in the fall, and 17 hours in the spring; pupae, 13 hours 20 minutes in the fall, and 17 hours 40 minutes in the spring; teneral adults, 13 hours 20 minutes in the fall, and 17 hours 50 minutes in the spring.

It is apparent from this data that if either temperature or photoperiod or a combination of both are the chief physical factors initiating diapause in *C. novem-*

notata, then the critical level of the factor, or factors, must be different for the spring and fall generations. Masaki (1953) has reported that in southern Japan the pupae of the spring generation of *Barathra brassicae* L. aestivate and those of the fall generation hibernate, a situation similar to that described here. Photoperiod, 16 hours of light inducing aestival diapause and 12 hours of light inducing hibernal diapause, was reported to be the principle factor governing the induction of diapause, although temperature also influenced the main photoperiod effect. Laboratory experiments determining the stage of development of *C. novemnotata* susceptible to diapause-inducing factors, and the levels of photoperiod and temperature effective for inducing diapause, will be described in a later paper.

Hagen (1962) has postulated that the aestival diapause of *C. novemnotata* and the aestivo-hibernation of some other coccinellids are adaptations for survival during seasons when prey are scarce. Reviews of literature by Gordon and Sampson (1939) and Burcham (1957) concerning the composition and seasonal growth patterns of native vegetation in central California lends support to Hagen's theory. Typically, the native vegetation is mature and dry from late June or early July until late September over most of the valleys and foothills, and is unsuitable for the growth of aphid populations. Periods of lush growth of vegetation suitable for the support of aphid populations occur in the spring and fall and correspond with the reproductive cycle of *C. novemnotata.*

Data showing the relative abundance of the pea aphid, the spotted alfalfa aphid and the feeding stages of *C. novemnotata* in an alfalfa field are shown in Fig. 1. Reproduction by the pea aphid is favored by cooler temperatures of the spring and fall months and is drastically checked by extremely hot summer temperatures (Campbell 1926). Thus its seasonal population distribution in irrigated alfalfa fields resembles that of aphids on the native vegetation. The spotted alfalfa aphid, *Therioaphis maculata* (Buckton), in contrast to the pea aphid is favored by hot summer temperatures, and when not suppressed by predation and parasitism may become very abundant during the summer months.

Hagen (1962) has observed that if spotted alfalfa aphids are abundant when adult *Hippodamia convergens* and *H. quinquefasciatus punctulata* emerge in the late spring then these normally univoltive species do not enter diapause but instead reproduce a second atypical generation. Hagen postulates that diapause in *Hippodamia* is facultative and largely determined by nutrition. In July and August of 1962 a second atypical generation of *H. convergens* was observed in the alfalfa field from which the data for Fig. 1 was obtained, even though the aphid population fell to relatively low numbers. The fact that in the same field *C. novemnotata* did not produce an atypical midsummer generation suggests that the diapause regulatory mechanisms for the two species are different, and that diapause in *C. novemnotata* is obligatory. Food supply as a factor influencing diapause initiation in *C. novemnotata* will be discussed in a later paper.

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Notes on the Biology of the Pitted Ambrosia Beetle, *Corthylus punctatissimus* (Coleoptera: Scolytidae), in Ontario and Quebec

R. J. FINNEGAN

Forest Research Laboratory, Department of Forestry and Rural Development, Sillery, Quebec

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The pitted ambrosia beetle, *Corthylus punctatissimus* (Zimm.), was studied during widespread infestations in sugar maple (*Acer saccharum* Marsh.) stands of southern Ontario and Quebec. A brief description of each stage of the insect is given, and its life history and habits, as well as the damage caused to the host plant are discussed.

Introduction

The pitted ambrosia beetle, *Corthylus punctatissimus* (Zimmerman), is indigenous to eastern North America, and has been reported attacking the following plants: maple (*Acer*); dogwood (*Cornus*); sassafras (*Sassafras*); hornbeam (*Carpinus*); elm (*Ulmus*); hophornbeam (*Ostrya*); hazel (*Corylus*); huckleberry (*Gaylussacia*); azaleas and rhododendron (*Rhododendron*); blueberry (*Vaccinium*); and mountain mahogany (*Cercocarpus*) (Weiss 1916; Soraci 1937; Robert 1947; Craighead 1949; Finnegan *et al.* 1959). Although the beetle usually occurs in small numbers on these plants, on several occasions it has been sufficiently abundant to cause considerable damage to and mortality of maples and rhododendrons (Merriam 1883; Twinn 1935; Daviault 1947, 1948; Boyd 1953).

In 1959 such an infestation in maple regeneration (*Acer saccharum* Marsh.) was observed over an extensive area in southern Ontario (Finnegan *et al.* 1959). This paper presents the result of investigations of *C. punctatissimus* during 1959 and 1960 in southern Ontario, and during 1961 and 1962 in southern Quebec.

Methods

The seasonal history of the insect was determined by sectioning 100 infested young maple plants collected weekly from mid-April to the end of September in 1959, and from the first week in April until mid-September in 1960. The overwintering status was established by examining infested stems collected in November 1959, and again in February 1960. The flight period was obtained by setting up eight windowpane traps in a heavily infested maple stand near Stayner, Ontario, during the summer of 1960. These traps were a modified version of that described by Chapman and Kinghorn (1955). The sheet of glass measured 2 feet by 3 feet, and was held by a wooden frame in a metal tray partly filled with water and detergent. The bottom edge of the glass was immersed in the liquid (Fig. 1). To reduce the possibility of error from directional variations in the flight path of the insect, four traps were set to face in the north–south direction and four were set to face in the east–west direction. The extent of