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INTRODUCTION

THE APHIDOPHAGOUS GENUS *Hippodamia* Dejean is not a large genus in number of species, but it is one of the commonest coccinellid genera in distribution and abundance of individuals, especially in the New World. In spite of their importance as natural enemies of many destructive pests, the biology of the aphid-feeding Coccinellidae has not received adequate attention from entomologists. Much of the importance given to Coccinellidae is based on scattered field observations or on inferences from studies of related species.

Hippodamia quinquesignata (Kirby) is largely a western species in the United States. The form used in this study was closest to the *punctulata* of LeConte (1852), which was redescribed by Chapin (1946). Typically, it does not possess the white converging lines on the thorax nor any black elytral markings. However, a very few individuals reared in stock colonies had converging lines similar to those possessed by *ambigua* LeConte. The stock colonies were established from adult beetles collected in alfalfa fields in central California and maintained on pea aphids, *Macrosiphum pisi* (Kaltenbach). The experiments were carried out in the insectary laboratories of the Department of Entomology and Parasitology, University of California, Berkeley.

FEEDING BEHAVIOR AND CAPACITY

Among the few contributions which pertain to the feeding behavior and capacity of coccinellid species including *H. quinquesignata* is that of Clausen (1916). His investigations, which were carried out under room conditions, revealed valuable biological information about life cycles and feeding rates, but probably more significant are the comparisons between species which can be concluded from his data.

Observations made throughout the present investigation indicate that a *H. quinquesignata* larva may feed on any part of the prey's body which is near its mouthparts at the time of capture. Once an aphid was captured, the larva inserted its mouthparts into the aphid's body and began feeding. First and early second instar larvae fed only on the body fluids of the aphid and discarded the shriveled skeleton, but the older larvae consumed, in addition to the body fluids, the skeleton, in part or completely. Later instar larvae, especially the third and fourth instars, ate almost the entire aphid, leaving only parts of the appendages, and even the appendages were eaten when larvae were given very few aphids. During the course of feeding, the larva occasionally pumped some of the ingested fluid from its own alimentary canal into the body of the host insect, then sucked it back. It repeated this regurgitating and reabsorbing many times until all the body fluids of the aphid were imbibed by the larva. As a result of this

feeding action, the aphid's body was inflated and deflated alternately. Hungry larvae did not always practice this type of feeding with the first few aphids captured, which were eaten rapidly with no apparent external digestion. Subsequently, as feeding slowed down, this phenomenon became evident. The larva, while feeding, fastened its abdominal tip to the substrate and held the aphid with its mouthparts reinforced by its forelegs. The younger larvae used their forelegs for this purpose more often than did the older larvae.

Larvae receiving small numbers of aphids searched and fed incessantly during their active feeding period. Those which found large numbers of aphids fed only at intervals. At 86° F, fourth instar larvae which had an unlimited number of aphids spent on the average 5.8 hours daily in actual feeding and 18.2 hours quiescent. The active feeding period is contrasted to inactive periods which shortly precede and follow the ecdyses. The inactive period which precedes the ecdyses is longer than that which follows it.

Feeding Rates

Methods.—The cages used were made from ⅛ inch Plexiglas sheets cut into 1½ inch squares with a hole in the center. The holes in size number 1 and 4 cages were cylindrical, ⅛ of an inch in diameter for size 1 and ¾ of an inch for size 4. In sizes 2 and 3, the holes were tapered, 5/16 of an inch in the upper diameter and 3/16 in the lower diameter for size 2; 7/16 in the upper diameter and 5/16 in the lower diameter for size 3. Each cage was covered with a Plexiglas sheet of similar size and center hole; this hole was covered with a fine cloth for ventilation.

A ladino clover leaflet was placed on a piece of balsa wood and covered with the cage. The petiole of the leaflet was inserted in a standing vial filled with water to keep it suitable for aphid feeding (pl. 21). The experiments started with 12-hour-old larvae confined singly in size 2 cages with second instar pea aphids, *M. pisi.* As larvae grew, other cages appropriate for their sizes were used. Size 2 cages were used for first and second instars, size 3 cages for third instars, and size 4 cages for fourth instar larvae. Later, fourth instar larvae were caged in double-depth cages. This method of caging and feeding was followed in all feeding experiments.

The feeding capacity (maximum rate) was studied at constant temperatures of 50° F (10.0° C), 60° F (15.6° C), 80° F (26.7° C), 86° F (30.0° C), and 90° F (32.2° C). The relative humidities at these temperatures were approximately 50, 38, 35, 35, and 31 per cent. The feeding capacity of the larvae at 86° F is considered the standard for various comparisons; hence, feeding studies were conducted at 86° F unless otherwise specified. All feeding experiments, except those on host preference, were carried out in the dark. The number of aphids varied with the experiments and ages of the larvae. In the experiments on feeding capacity (maximum rate of feeding) more aphids were provided than the larvae could kill, and yet not enough to crowd the cages. Larvae during the fourth instar and at temperatures of 80°, 86°, and 90° F were given aphids twice a day, but at earlier stages at these same temperatures larvae were supplied with aphids only once a day. The daily counts included the number of aphids alive, those dead from natural causes, and those killed by the coccinellids. Every other day, the

larvae reared at 50° and 60° F were checked, and the aphids were counted and replaced.

The aphids killed were classified arbitrarily into four classes according to the degree of consumption, that is, less than half consumed equals one food unit; half consumed equals two food units; more than half consumed equals three food units; and entirely consumed has a value of four food units for each aphid. The total food units for each larva divided by four gives the number of aphids consumed for that period. Both the total number of aphids killed and the number consumed were used for comparison. The number of aphids killed indicates the effectiveness of the larvae as predators, and the number consumed represents the quantity of food ingested. The larval period used to calculate the daily rates was the larval feeding period; this did not include the prepupal period.

Second instar pea aphids, *M. pisi,* were chosen as food for the larvae because of their availability in aphid stock colonies and their nonreproducing status during the experimental periods. These young aphids were on the average one-fifth the weight of the adult *M. pisi.*

Clausen (1916), in his study of some aphidophagous cocinellid species, considered the number of the dead aphids during the confinement period (24 hours) minus the number of naturally dead aphids in the check cages for the same period as the number of aphids killed by the larvae. This method was not adopted here because the natural mortality in the check cages was variable and sometimes high, and this method does not show quantitatively the food consumed. Also, the aphids which died are easily distinguished from those killed by larvae. Putman (1957) analyzed the frass of coccinellids to determine the number of aphids eaten. He counted the more heavily sclerotized and easily identified fragments of the consumed aphids such as the tips of the rostrum and the tarsi. Putman's method could not be used here either, because it does not actually indicate the quantity of food consumed, for the larvae in earlier instars and sometimes during later instars feed on the aphid's body fluids and discard its skeleton. Furthermore, the larger larvae that consume the skeleton usually do not feed on the heavily sclerotized parts of the aphids unless the number of aphids available is very low.

Maximum rates of feeding.—Rates of larval feeding when an unlimited supply of aphids was available were generally correlated directly with the temperature; low rates at low temperatures and higher rates at higher temperatures up to 86° F where the maximum rate of feeding occurred. At 90° F the feeding rate declined (table 1 and fig. 1). This pattern is indicated when the daily average for the total larval life at each temperature is considered, but it deviated slightly when the daily averages for each instar are compared. At 86° F, the feeding rate for the third instar was lower than the rates at 80° and 90° F. The lowest rate was at 60° F. At 80° and 90° F, the rates were about the same for the first and third instars, but higher at 80° than at 90° F for the second and fourth instars (fig. 2). Differences in the total number of aphids killed or consumed at various temperatures were not as striking as the daily rate of feeding. These values were 224.7, 258.6, 235.9, and 190.8 for aphids killed, and 190.3, 241.4, 215.6, and 158.2 for aphids consumed at temperatures of 60°, 80°, 86°, and 90° F. The threshold temperature for feeding and development seems to be near 60° F. At 50° F the larvae

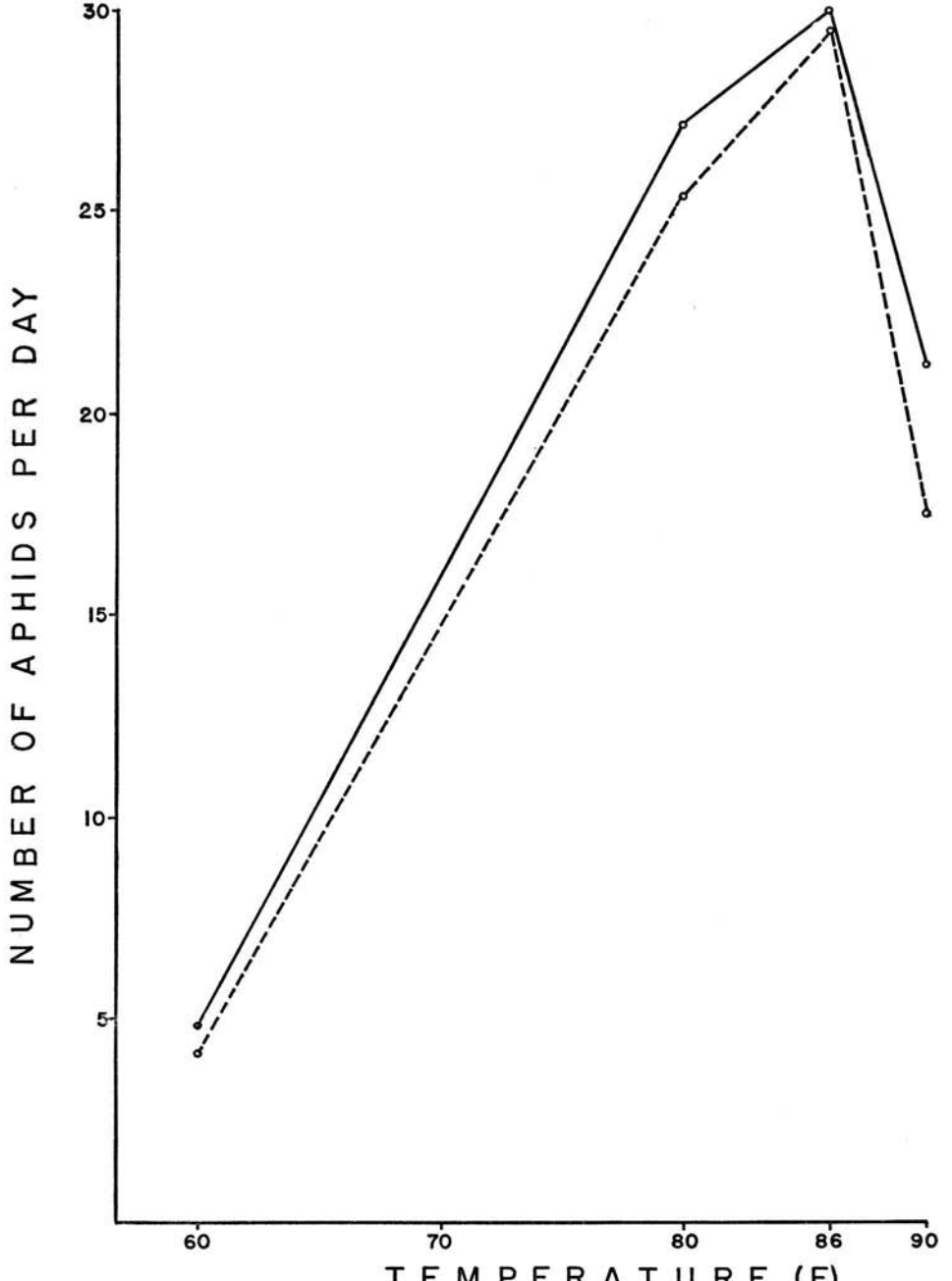

Fig. 1. The maximum feeding rates of *H. quinquesignata* under various constant temperatures in degrees Fahrenheit. The solid line represents the number of aphids killed, the broken line the number of aphids consumed.

were inactive and apparently unable to feed actively. Occasionally at this temperature some larvae were noticed holding aphids and feeding very slowly, and the bodies of these larvae seemed slightly distended, an indication of having fed. The aphids killed were almost intact except for small feeding punctures in their bodies. Eventually, all larvae at this temperature died during the first instar. The average longevity at 50° was 34 days (range 7 to 51); the average number of total aphids killed was 4.0; the average total aphids consumed was 1.0 aphid. Tests conducted at a temperature of 99° F (37.2° C) indicated that larvae fed on aphids, but the feeding and development were retarded. None of the ten larvae observed completed development. Most of the mortality occurred during the first and second instars. No data regarding quantity of food consumed are available from this test.

The total time of development (table 2 and fig. 3) is similarly correlated with the temperature, but inversely; shorter durations are found with higher temperatures up to 86° F, then slightly lengthened at 90° F. This correlation has some exceptions in the data for the various instars. The duration of the first instar and of the prepupal and pupal periods was shorter at 90° F than at 86° F, and the first instar lasted just as long at a temperature of 80° F as at 86° F.

Male and female larvae exhibited different rates of feeding (table 3). For the temperatures 60°, 80°, and 86° F, total and daily food consumption and weights of pupae and adults were higher for the female than male larvae. Larval periods were equal at 80° F and shorter for male than for female larvae at 60° and 86° F. This pattern is reversed at a temperature of 90° F; male larvae ate more aphids, had heavier pupae and adults, and longer larval periods than female larvae.

Comparison to Paranaemia.—Larvae of *Paranaemia vittigera* (Mannerheim) had lower feeding capacity than larvae of *H. quinquesignata* reared under the same conditions (temperature 86° F, relative humidity 35 per cent, and no light, table 4). The total aphids killed and aphids consumed were about the same for the two species but the daily consumption (total average) is lower for *P. vittigera* than for *H. quinquesignata.* By comparing the rate of feeding at various instars for the two species, again as with the temperature, the rate at the third instar of *H. quinquesignata* is lower than the corresponding rate of *P. vittigera.*

Effects of submaximal feeding.—Larvae were reared on various amounts of food which ranged from near the minimum for survival to the maximum as described above. The most critical test was that of minimum food. Larvae in this test received one aphid a day during their first three instars and two aphids a day during the fourth instar.

The results indicate delayed development and high mortality at this low level of feeding. Only 3 larvae completed development out of an initial 32. Most of the mortality occurred shortly before or after ecdyses. In general, there was a good correlation between the amount of food (number of aphids consumed) and time of development (or rate of growth) of the immature stages, and also between the amount of food consumed and weights of pupae and adults (table 5). The gain in weight and in speed of development which resulted from increase in the amount of food received by the larvae was at first rapid, then slowed as the maximum limit was approached. In other words, this gain was not proportional to the amounts of food consumed by the larvae.

TABLE 1

MAXIMUM RATE OF FEEDING OF *H. quinquesignata* LARVAE ON *M. pisi* UNDER VARIOUS CONSTANT TEMPERATURES (F)

Instar[a]	Aphid mortality per day				Aphid consumption per day			
	60	80	86	90	60	80	86	90
First	0.9	3.5	5.3	3.3	0.2	1.0	1.6	1.0
Second	1.6	11.6	14.9	8.2	0.5	8.4	11.0	5.3
Third	4.0	22.6	19.9	23.4	2.8	21.4	16.8	20.4
Fourth	8.3	59.2	74.9	39.3	7.9	58.5	73.8	33.8
Total feeding period	4.8	27.2	32.3	21.2	4.0	25.4	29.5	17.6

[a] Number of larvae observed were 15, 14, 13, and 11; 10, 10, 10, and 9; 10, 10, 10 and 10; 15, 14, 14, and 12, for the four instars at the respective temperatures of 60°, 80°, 86° and 90°F.

TABLE 2

TIME OF DEVELOPMENT AT VARIOUS CONSTANT TEMPERATURES OF *H. quinquesignata* IMMATURE STAGES

Number of insects observed	Temp. (F)	Average duration of stages (days)								
		Instar				Total larval period[a]		Pupal	Total immature	S.D.[b]
		First	Second	Third	Fourth	Feeding larvae	Pre-pupae			
11	60	9.8	8.1	9.4	19.9	46.6	3.3	17.9	67.8	0.63
9	80	2.5	2.0	1.9	3.1	9.5	0.9	5.1	15.5	0.00
10	86	2.5	1.0	1.4	2.4	7.2	0.8	3.1	11.1	0.15
12	90	2.3	1.4	2.3	3.0	9.0	0.5	2.9	12.4	0.34

[a] Feeding larvae refers to the larval period preceding the prepupation.
[b] S.D. This is the standard deviation of the mean, or the standard error, of the total immature period.

TABLE 3

MAXIMUM RATES OF FEEDING AND RATES OF DEVELOPMENT OF IMMATURE STAGES AND WEIGHTS OF PUPAE AND ADULTS OF MALE AND FEMALE LARVAE REARED UNDER SIMILAR CONDITIONS

Temp. (F)	Sex and number observed	Average aphids consumed		Average developmental periods (days)		Average weights (milligrams)	
		Total	Daily	Larval	Total	Pupae	Adults
60	Male (4)	173.9	3.8	46.0	66.5	14.9	13.1
	Female (7)	198.9	4.2	46.9	67.2	19.6	15.1
80	Male (6)	232.2	24.4	9.5	15.0	23.3	16.4
	Female (3)	260.6	27.4	9.5	15.0	26.6	17.7
86	Male (4)	192.6	27.1	7.1	10.6	21.0	16.6
	Female (6)	238.3	32.6	7.3	10.6	25.0	20.0
90	Male (4)	201.5	23.1	8.8	11.9	19.1	14.6
	Female (8)	166.5	19.8	8.4	11.9	18.0	13.4

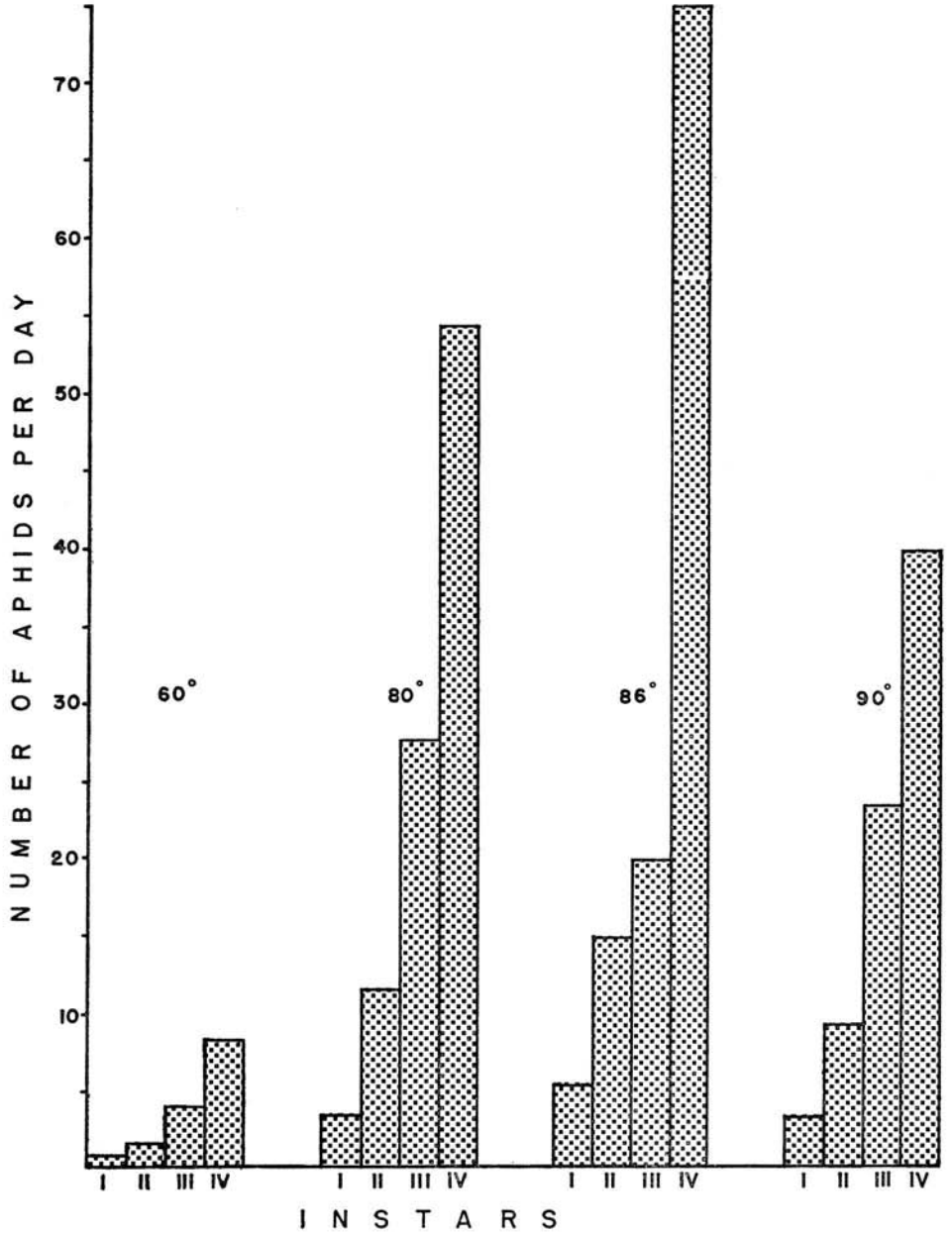

Fig. 2. The maximum feeding rates (number of aphids killed) of the four larval instars of *H. quinquesignata* under various constant temperatures, degrees Fahrenheit.

TABLE 4

COMPARISON OF LARVAL MAXIMUM FOOD CONSUMPTION OF *Hippodamia quinquesignata* (KIRBY) AND *Paranaemia vittigera* (MANNERHEIM) (86°F and 35 per cent humidity)

Food consumption	*P. vittigera* (n = 6)	*H. quinquesignata* (n = 10)
FIRST INSTAR		
Duration—days	2.5	2.5
Aphids killed per day	3.2	6.6
Aphids consumed per day	1.7	1.9
SECOND INSTAR		
Duration—days	2.0	1.0
Aphids killed per day	9.7	14.9
Aphids consumer per day	7.6	11.0
THIRD INSTAR		
Duration—days	2.0	1.4
Aphids killed per day	33.3	19.8
Aphids consumed per day	29.2	16.8
FOURTH INSTAR		
Duration—days	3.0	2.4
Aphids killed per day	45.7	74.9
Aphids consumed per day	41.6	73.8
LARVAL TOTAL		
Duration	9.5	8.1
Aphids killed	229.9	235.9
Aphids consumed	202.5	215.6
Aphids killed per day	25.5	35.6
Aphids consumed per day	22.4	31.7

Effects of starvation.—Two groups of larvae were subjected to various degrees of starvation. The first group (11 larvae) was given one aphid a day during the first three instars, and the maximum feeding capacity was determined during the fourth instar. Only 4 larvae out of this group completed development to adults; the others died during the course of starvation. The second group of larvae (7 larvae) was reared on a maximum number of aphids during the first three instars, followed immediately after the third ecdysis by a 48-hour period of complete absence of aphids. Then the maximum feeding capacity was established during the remainder of the fourth instar period. Six larvae of this group completed development to adults, and only one died. Results of these two starvation

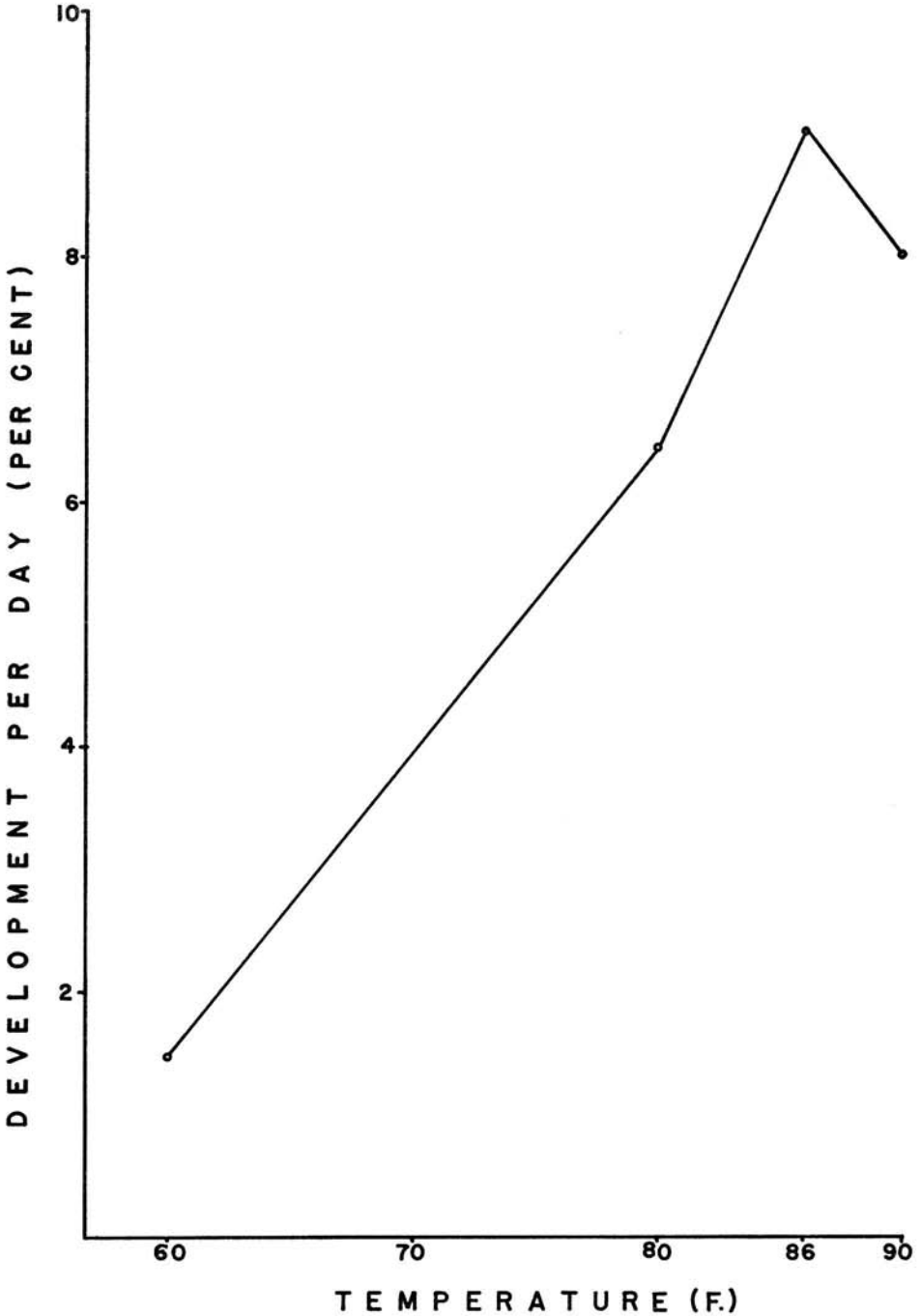

Fig. 3. Growth rate of *H. quinquesignata* larvae at different constant temperatures, degrees Fahrenheit.

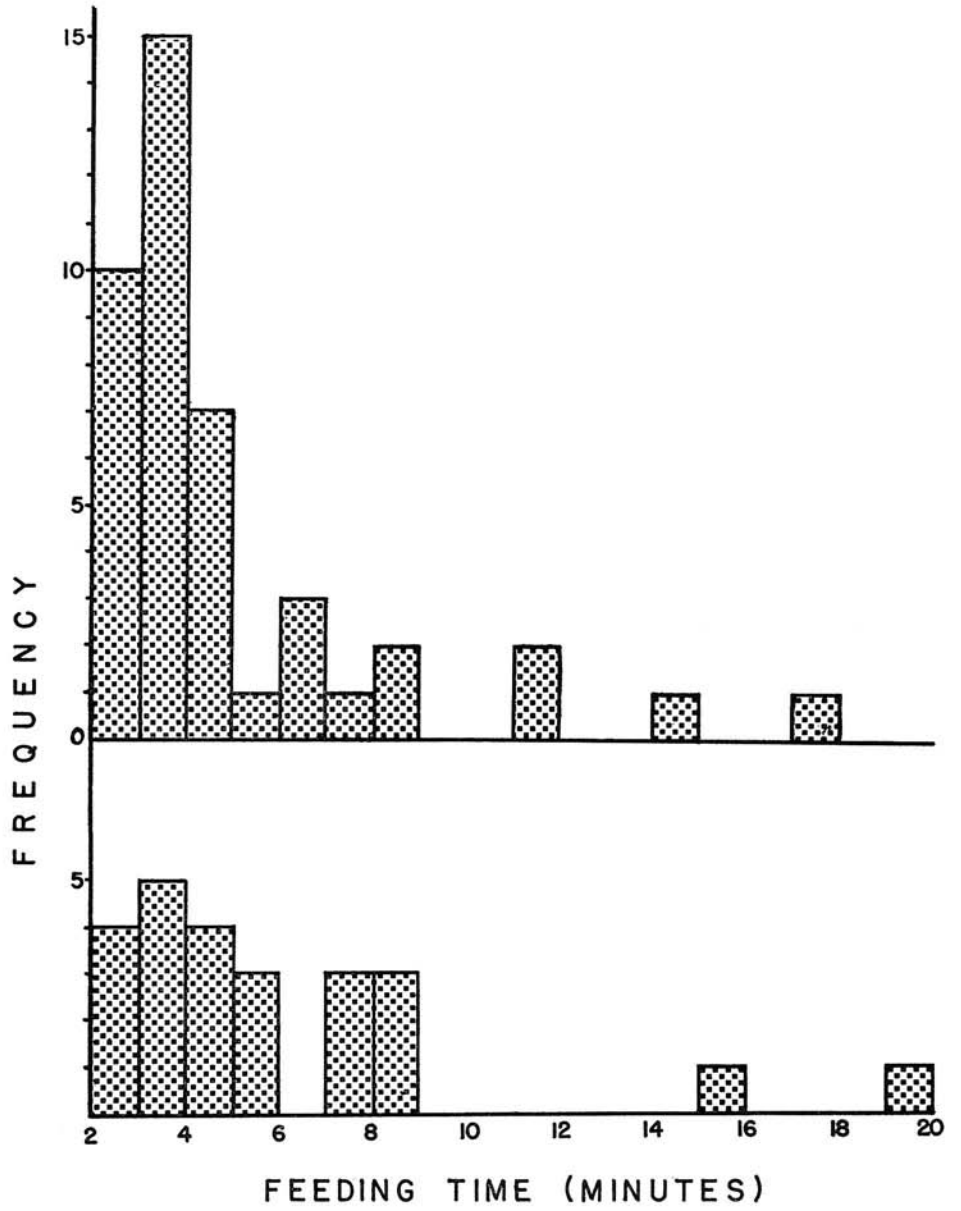

Fig. 4. A histogram representing the frequency of feeding times of the fourth instar larvae of *H. quinquesignata* on *M. pisi* (above) and on *T. Maculata* (below).

tests are compared with the basic group of larvae which was fed on maximum amounts of food continuously at 86° F (see Maximum Rate of Feeding, p. 183); all tests were carried out under similar physical conditions.

Starvation resulted (table 6) in smaller insects with lower feeding capacities than the nonstarved group. This adverse effect of starvation is correlated with the degree of starvation. Mortality is another manifestation of this adverse effect.

TABLE 5

RELATION OF FOOD CONSUMPTION DURING LARVAL PERIOD TO LENGTH OF DEVELOPMENT OF IMMATURE STAGES AND TO WEIGHTS OF PUPAE AND MATURE INSECTS
(at 86° F)

Number of larvae observed	Aphids consumed[a]		Duration of stages — days			Weight (milligrams)	
	Per day	Total	Larval[b]	Pupal	Total	Pupal	Adults
3	1.2	32.3	27.0	4.0	31.0	5.4	4.5
8	15.5	131.7	8.5	4.0	12.5	17.6	14.1
5	23.4	191.8	8.2	3.8	12.0	20.5	16.6
10	29.5	215.6	8.1	3.1	11.2	23.1	18.7

[a] The daily aphids killed for the respective groups are 1.3, 17.9, 25.1, and 32.3.
[b] This includes the prepupal period.

TABLE 6

FEEDING CAPACITY AND WEIGHTS OF PUPAE OF *H. quinquesignata* IN RELATION TO VARIOUS DEGREES OF STARVATION DURING THE LARVAL PERIOD

Number of larvae observed	Aphids consumed during the first three instars		Starvation period (days)	Aphids consumed during the fourth instar		Weights of pupae (milligrams)
	Per day	Total		Per day	Total	
4	0.9	18.5	0	17.1	59.9	10.7
6	...[a]	....	2	39.5	137.9	19.7
10	8.7[b]	38.4	0	73.8	177.2	23.1

[a] This group of larvae were fed on maximum amounts of food during the first three instars (comparable to the amount consumed by the last group of larvae) but the exact number of aphids consumed was not determined.
[b] This is the standard group of larvae which were fed on maximum amounts of food, and were not subjected to any starvation.

HOST PREFERENCE

Hippodamia quinquesignata is normally an aphid-feeding species. Its host range, at least as reported in the literature (see table 8), is not as great as that of *H. convergens* Guérin. This is probably a result of the wider distribution of the latter species and the lack of a complete study of the feeding habits of the former.

Many aphidophagous coccinellid species resort to other sources of food when their normal host insects are scarce. *Leis conformis* (Boisduval) obtained nourishment from extra floral nectaries of *Crotalaria* species, pollen of saw palmettos, the tender terminal buds of scrub oak, sap from pruning wounds of tangerine trees, and the blossoms of fireweed including the pistils and stamens (Watson and Thompson, 1933). Stomachs of larvae and adults of *H. convergens,* upon dissection, were found by Forbes (1883) to contain food of both animal and plant origin.

Animal types of food included aphids, mites, millipedes, caterpillars, chinch bugs; of plant origin were fungus spores, pollen, and lichens in various proportions. The ability of some coccinellid species to utilize food of both plant and animal sources is considered by Forbes (1880) as advantageous, for those species are better able to maintain higher population than would be possible if they were entirely dependent on animal food alone. Balduf (1935) concluded that coccinellid larvae generally feed on the same type of food as the adults eat.

Not all species of aphids are equally preferred by the aphidophagous Coccinellidae, nor are they equally suitable as hosts. A predator may not prefer a host insect because of its suitability as a host. Similarly, preference for a host insect may not be indicative of its suitability for the normal development of the predator. A complete study, rather than scattered field observations, is required in order to evaluate properly the relation between an insect species and its associated entomophagous species. According to Campbell (1926), although lady beetles do not attack pea aphids *Macrosiphum pisi* as readily as other species of aphids, they can still be found in infested pea fields, occasionally in large numbers, feeding on pea aphids. *Adalia bipunctata* (Linnaeus) feeds on a large number of aphid species but not on all of them. Some of its nonpreferred aphid species are *Aphis fabae* Scopoli (as *A. rumicis* Linnaeus), *Macrosiphum aconitum* (Van der Goot), *Hyalopterus arundinis* (Fabricius) [as *H. pruni* (Geoffroy)], and several other highly colored aphids. The last species has gray-green exudation which plugs the mouthparts of the larvae and thus causes their death (Hawkes, 1920). Large aphids such as *Macrosiphum rudbeckia* (Fitch) and *M. ambrosiae* (Thomas) smeared the mouthparts of *H. convergens* with glue exuded from the aphid cornicles, and thus caused starvation of the predator (Palmer, 1914). The harmful effects of this glue seem to take place only at low temperatures when activities of beetles are curtailed, for at higher temperatures the beetles can ingest the glue secreted by aphids. *Coccinella septempunctata* Linnaeus reared on *Aphis sambuci* Linnaeus had a much lower rate of feeding, slower rate of development, and eventually ended with 100 per cent mortality compared to a check group of larvae which developed normally on *Doralis* species (Hodek, 1956). According to Hodek, the probable cause of this adverse effect is the glycoside, sambunigrin, present in the elder—the host plant of this aphid—and transferred to the body of the aphid where it is split by enzymes to cyanic acid.

Entomophagous insects with a wide host range are apt to have wide variations in their morphological and biological qualities. Rate of development of larvae, longevity, anatomical measurements, and color of adults of *Chrysopa cubana* Hagen (as *Chrysopa lateralis* Guerin) are affected by the variations in the larval food (Muma, 1957).

Pea aphids vs. spotted alfalfa aphids.—Fourth instar larvae starved for 24 hours were used for host preference tests. Each was maintained in a cage (size number 3) with 5 adult apterous spotted alfalfa aphids, *Therioaphis maculata* (Buckton), and 5 pea aphids, *M. pisi,* of size similar to the spotted alfalfa aphids. The cage was ventilated through a cloth bottom, and its upper side was covered with transparent Plexiglas through which observations were made. The caged larvae, tested one at a time, were under continuous observation through a binocular

microscope. Aphids captured and eaten were immediately replaced by others of the same species and size and, when practical, remains of killed aphids were removed from the cage. These tests were conducted at a temperature of 81° ± 1° F (27.2° ± 0.6° C), relative humidity of 38 per cent, and incident light of 60 foot-candles.

During the first part of confinement, larvae captured aphids rapidly and indiscriminately with reference to species. After their hunger was partly satisfied, larvae seemed to exhibit a slight preference for pea aphids over spotted alfalfa aphids (table 7). The same results were obtained with larvae reared on pea aphids and with those reared on spotted alfalfa aphids. Also, results of 30-minute tests

TABLE 7

FEEDING REACTION OF FOURTH INSTAR LARVAE OF *H. quinquesignata* TO *M. pisi* AND *T. maculata*

Number of larvae observed	Exposure time (minutes)	Aphids contacted (average)		Aphids consumed (per cent)		Aphids rejected (per cent)
		Species	Number	Completely	Partly	
4.....	30	*M. pisi*.....	7.5	93.3	6.7	0.0
		T. maculata.....	6.8	77.8	18.5	3.7
7.....	60	*M. pisi*.....	7.6	87.0	9.4	3.6
		T. maculata.....	8.9	42.0	29.0	29.0
3[a].....	60	*M. pisi*.....	6.3	94.7	5.3	0.0
		T. maculata.....	4.3	69.2	30.8	0.0

[a] This group of larvae were reared on spotted alfalfa aphids, whereas the others in this table were reared on pea aphids.

were of similar pattern as the 60-minute tests. In the latter tests larvae had a longer time to practice selective feeding after the period of wild hunger was past.

The time required to consume an aphid was very short at first, then prolonged as time advanced and the larvae approached satiation. The range and frequency of feeding times of larvae on pea aphids and spotted alfalfa aphids are shown in figure 4. Statistical analysis of these two sets of feeding times on the two aphid species, however, showed that they are not significantly different. Therefore it will be assumed that time of feeding is not a function of aphid species.

Feeding on dead aphids.—Twelve-hour-old first instar larvae were each given 3 fourth instar newly dead and slightly discolored pea aphids. The number of aphids increased with the age of the larvae. No data on quantitative food consumption is available; only larval development was recorded. This test was carried out at a constant temperature of 86° F, relative humidity of 35 per cent, and no light.

The larvae fed on the dead aphids, but the results indicate that this type of food is unsuitable for development. The detrimental effect of dead aphids was manifested especially during later instars when larvae require larger amounts of food than earlier instars. Out of a total of 10 larvae, 3 died during the first instar, 5 died during the second, one in the third, and one in the fourth instar. The average longevity of these larvae was 5 days (3 to 10).

Some larvae in the stock colonies were seen feeding on dead aphids when aphids were scarce, especially on recently dead and slightly discolored aphids.

Discussion

The larvae of *H. quinquesignata* do not begin feeding after hatching until they are one or two hours old. They may feed during the clustering period on eggs of their own egg clusters or of neighboring clusters. Subsequent to the clustering period, larvae disperse, searching for aphids or other sources of food. (See Searching Capacity, p. 197.)

The feeding behavior of larvae reflects their piercing, chewing mouthparts. This chewing ability develops gradually with the age of the larvae. During the first and part of the second instars, feeding is accomplished mainly through piercing and sucking. Thereafter chewing ability appears and develops rapidly. Feeding during the later instars is through piercing-sucking and chewing. This type of feeding (external digestion) has been reported also for larvae of other species of insects such as the coccinellids *A. bipunctata, C. septempunctata,* and *Propylaea quatuordecimpunctata* (Linnaeus) (Banks, 1957), *Scymnus casstroemi* Mulsant (Smit, 1917), *Pullus impexus* (Mulsant) (Delucchi, 1954), and the larvae of the staphylinid, *Oligota oviformis* (Casey) (Quayle, 1913).

Larvae of *H. quinquesignata* do not feed during the inactive periods shortly before and after ecdyses. This is in agreement with the larval behavior of *Hyperaspis vinciguerrae* Capra (Hafez and El-ziady, 1952) and in partial agreement with the findings of Palmer (1914) who found a decline in feeding of *H. convergens* before molting. On the other hand, Clausen's (1916) results seem to contradict this conclusion. He studied several species of *Hippodamia, Coccinella, Olla, Adalia,* and *Cycloneda* and found that all these species, including *H. quinquesignata* and excepting *Coccinella californica* Mannerheim, fed normally up to the day of pupation and that no appreciable diminution occurred in the number of aphids eaten on the days of ecdysis. Clausen's records were obtained at room temperatures. The duration of the inactive period depends on existing conditions of temperature. It is shorter at higher temperatures than at lower temperatures; it was only a few hours at 90° F but extended to several days at 60° F.

Under constant temperatures, feeding activity is restricted between 60° F (about the threshold temperature for feeding and growth) and slightly below 99° F. The highest lethal low temperature is about 50° F, and the lowest lethal high temperature is about 99° F. Mortality caused by lethal low and high temperatures may be a result of starvation, as suggested by Huffaker (1944). On the basis of the growth rate and the maximum daily consumption, the optimum temperature for these larvae can be estimated. Among the temperatures studied, 86° F seems to be the optimum, as indicated by the shortest development time and the highest rate of aphid consumption. The predator population has the ability to respond faster to changes in the host population and to destroy larger numbers at high temperatures (up to the optimum) than at low temperatures. Temperature fluctuation may have a sitmulating effect on feeding capacity. Daily consumption of *C. septempunctata* fed on *Aphis fabae* (Scopoli) (as *Doralis fabae* Scopoli) was much higher (50.1 aphids) at an average temperature of 24.7 (range,

22.2 to 26.6° C) than at a constant temperature of 25.6° C (31.7 aphids) (Hodek, 1957).

The rate of aphid consumption of *H. quinquesignata* larvae increases with their age. Later instar larvae feed voraciously, kill large numbers of aphids, and consume most of them, especially when reared at favorable temperature conditions. This is in contrast to younger larvae which kill fewer aphids and partly consume them. Feeding is required at every instar, and no instar transforms to the next when food is completely lacking.

The rate of food consumption varies with the sex of the larvae. At temperatures of 60°, 80°, and 86° F, the female larvae have a higher rate of food consumption than the male, whereas at 90° F the male larvae have a higher rate of food consumption. This difference in the feeding capacity may lead to the conclusion that larvae with higher rates are more efficient in combating aphids than larvae with lower rates of aphid consumption.

Growth rates of the larvae (fig. 3) follow a pattern similar to that of feeding rates at the constant temperatures studied (fig. 1). This may indicate that growth of the coccinellid larva is largely dependent on the amounts of nourishment it obtains. Hence, growth rate decelerates at 60°, 80° and 90° F from that at 86° F because of partial starvation. This correlation between amounts of food received by larvae and growth rate is clearly indicated in the results shown in table 5. Larvae fed a small number of aphids developed more slowly than larvae that received larger numbers. Starvation has another harmful effect on larvae other than prolongation of the developmental time and mortality. Starved larvae, even if the starvation period is short, develop into individuals with lower feeding capacity than nonstarved larvae. Well-nurtured larvae develop into large individuals which require and are capable of consuming a larger number of aphids than larvae of smaller size developed on lower amounts of food. This suggests that larvae, in situations where aphids are very abundant, develop in the shortest time possible under the existing physical conditions. Hence, their life cycle is shorter and their feeding capacity is higher than at lower host population density. In other words, the action of the coccinellid larvae on its host populations is a density-dependent action.

H. quinquesignata larvae have a broad range in feeding rates and a well-developed tolerance to starvation. The daily consumption of aphids at 86° F ranged from 1.2 to 31.7 aphids. This broad range, the ability to survive at very low host densities, and the ability to destroy large numbers of host insects at high host densities are of primary biological significance. Fleschner (1950) pointed out that the ability of an entomophagous insect to survive at the lowest host density is not synonymous with its ability to destroy the surplus progeny of the host insect at the lowest host density, but it is considered the best criterion, however, for measuring this faculty by the use of larval population alone.

Larvae of *H. quinquesignata* have a rather wide host range which consists mainly of aphids but includes other species of insects and plants (table 8). Undoubtedly, they have various degrees of preference among these foods. Laboratory tests showed that larvae exhibited a slight preference for pea aphids over the spotted alfalfa aphids as mentioned earlier. The behavior of the larvae in

TABLE 8

LIST OF RECORDED HOSTS OF *H. quinquesignata* (KIRBY)[a]

Host species	Host plant	Locality	Coccinellid stage[b]	References
Aphidae				
Aphis favae Scopoli (as *A. rumicis* Linnaeus)	.....	California	L & A	Davidson, 1914
Anuraphis bakeri (Cowen) (as *Aphis bakeri*).....	Red clover	Idaho	L & A	Burrill, 1918
Capitophorus elongatus Knowlton.....	Rabbit brush	Utah	A	Knowlton, 1949
Chromaphis juglandicola (Kaltenbach).....	Walnut	California	L & A	Davidson, 1914
Hyalopterus arundinis (Fabricius).....	.....	California	....	Davidson, 1914
Macrosiphum cockerelli Hottes.....	Rudbeckia	Utah and Idaho	A	Knowlton, 1954
M. eoessigi Knowlton.....	.....	Utah	A	Knowlton, 1949
M. pisi (Kaltenbach).....	Peas	California	L & A	Campbell, 1926
M. pisi.....	Peas and others	North America	L & A	Fluke, 1929
M. pisi.....	Alfalfa	Utah.....	A	Knowlton, 1949
M. pisi.....	Vetch, peas, alfalfa and laboratory	Oregon	L & A	Rockwood, 1952
M. rosea (Linnaeus).....	Rose and laboratory	California	L & A	Russell, 1914, and Clausen, 1916
Monellia californica Essig.	Walnut	California	L & A	Davidson, 1914
M. caryae (Monell).....	Walnut	California	L & A	Davidson, 1914
M. caryella (Fitch).....	Walnut	California	L & A	Davidson, 1914
Myzus persicae (Sulzer)...	Sugar beet	Utah	L & A	Knowlton, 1949
Phorodon menthae (Buckton).....	*Mentha spicata*	Utah	....	Knowlton, 1949
Therioaphis maculata (Buckton).....	Alfalfa	California	L & A	Smith and Hagen, 1956
T. maculata.....	Alfalfa	California	L & A	Davis *et al.*, 1957
Coccinellidae				
Epilachna corrupta Mulsant (eggs).....	Beans	Southwest U.S.	....	Chittenden, 1919
E. corrupta (eggs).....	Beans	Colorado and neighboring states	....	Chittenden and Marsh, 1920
E. corrupta (eggs and young larvae).....	Field and laboratory	Florida	L & A	Howard, 1921
Psyllidae				
Paratriosa cockerelli (Sulc) (nymphs and adults).....	Laboratory	Utah	A	Knowlton, 1933
P. cockerelli.....	Solanaceae	Montana	L & A	Pletch, 1947
Curculionidae				
Hypera postica Gyllenhal (small larvae)	.....	Utah	A	Knowlton, 1949
Leguminaceae (plant source)				
?Nectaries at the stipules of vetch, alfalfa, and peas	.....	Oregon	....	Rockwood, 1952

[a] This list includes hosts of the two subspecies *ambigua* and *punctulata*.
[b] L = Larvae; A = Adults.

the field toward these two species of aphids, however, may not be consistent with their behavior in the experimental cages. The reaction of aphids approached by larvae may influence larval choice (see Host Finding, p. 207). Under the stress resulting from a scarcity of aphids, larvae resort to other sources of food including less preferred insect species, dead host insects, their own species, or even food of plant origin.

The comparative feeding capacity of some aphidophagous coccinellid larvae may be concluded from Clausen's (1916) investigation. The daily consumption of aphids is the lowest [the rose aphid, *Macrosiphum rosae* (Linnaeus) was used], and rate of growth is the slowest for larvae of *H. quinquesignata* than of any other species studied. According to these results it may seem that *H. quinquesignata* is inferior to those species as a natural enemy of aphids, at least in the larval stages and in combating the rose aphid. These, however, are not the only criteria on which the efficacy of an entomophagous insect should be judged. Host specificity, distribution (or tolerance limits to environmental factors), feeding capacity of the adult, fecundity, fertility, searching ability, and natural enemies are some of the other important factors that should be considered for evaluation of a natural enemy. In California, *H. quinquesignata* is one of the most important lady beetles controlling aphids on various field crops. Among Clausen's group of Coccinellidae, it probably ranks second in importance after *H. convergens* in controlling aphids in the field. The others are not abundant, not widely spread, or not aphid-specialized feeders. Another example where incomplete information may lead to the wrong conclusion is *Paranaemia vittigera*. Larvae of this species were reared and developed normally on *M. pisi* under laboratory conditions. They consumed large numbers of aphids, their feeding capacity being slightly below that of *H. quinquesignata* larvae. In alfalfa fields, however, *P. vittigera* is considered of minor importance as a natural enemy of aphids because it is not abundant and not an aphid-specialized feeder. A direct comparison of feeding rates obtained by Clausen (1916) and those from this study is not possible. Different techniques and different aphid species were used in the two investigations.

SEARCHING CAPACITY

One of the qualities that determine the efficacy of a predator or a parasite as a natural enemy is its searching capacity. At high host density both a poor searcher and a more efficient one destroy hosts at their maximum potential; but searching capacity becomes of prime importance when host density is low. An efficient searching entomophagous insect can find and utilize its host at a low density level. It may be able to destroy sufficient numbers to hold the level of its host below the economic threshold, whereas an inefficient searcher with equal reproductive potential cannot.

The attributes which influence searching capacity of an entomophagous insect are of two kinds, intrinsic and extrinsic. Among the intrinsic qualities are the mobility of the predator or the parasite, its power of perception, its power of survival, its aggressiveness and persistence (Smith, 1939), and its ability to coincide with the host geographically, seasonally, and ecologically (Salt, 1935).

Among factors of an extrinsic nature is the dispersion of the host rather than its average population density (Smith, 1939). Smith believed that the more the dispersion of a host tends to be of a colonial type, the more efficient is its entomophagous enemy. In other words, control of a uniformly dispersed host insect requires an entomophagous enemy with a higher power of host discovery than does a host of a colonial type distribution. According to Smith, differences in dispersion pattern of the host resulted in success of *Rodolia cardinalis* (Mulsant) on cottony cushion scale and failure of *Rhizobius ventralis* (Erichson) on black scale. Population densities of the host and its natural enemies are among the important factors which interact upon each other to produce the final impact of the natural enemy on its host. The higher the density of the host insect or its entomophagous enemy, the higher the rate of host discovery will be (De Bach and Smith, 1942). This is true up to a certain level. These authors added that the rate of host finding, although increased with the increasing host density, is not a constant, but decelerates and finally levels off. Similarly, increase in parasite density, up to a certain point in relation to that of its host, results in an increase of the parasite population (De Bach and Smith, 1947). Beyond this point, any increase in parasite population results in lower rates of host finding. They attributed this behavior to competition, overlapping in searching for the host, and to the increase of superparasitism with the higher parasite population density which all lead to a decrease in the parasite population in the subsequent generations. Environmental conditions such as light, temperature, and humidity also affect searching capacity (Laing, 1938). Kinetic and directional influence of the physical factors modify insect behavior and, accordingly, its rate of success in finding its prey.

Smith (1939) stated that predators are inferior to parasites in controlling pest insects. Predaceous larvae have to find successive hosts in order to reach maturity. Where the mobility of these larvae is limited they will be inefficient. In contrast, only one host is needed for the parasitic larva, and this is found by its mother, the female parasite with good powers of flight.

On the basis of this relation to their host insects, coccinellid larvae range from highly specialized forms approaching parasites, to nonspecialized forms such as the aphid-feeding species. In general, the closer their habits are to those of parasites the more effective the species will be in controlling their host insects. The adult beetle of *R. cardinalis*, an active flier, finds the food on which its progeny is to develop before oviposition. The egg is laid on the adult female host insect or upon the egg mass where there is sufficient food material for the predaceous larva to complete its development (Clausen, 1940). Thus the larva does not have to search for food, and its development is assured by the activity of its mother. As a result of this habit, at least in part, this species of Coccinellidae is able to maintain itself on a very low level of host population. Similar to this, with some modification, are some coccinellid predators of diaspine scale insects and white flies. The gregariousness of these host insects, exhibited even when their population is very low, enables the coccinellid larvae to encounter their hosts with a minimum amount of searching (Clausen, 1940). The habits of these predators approach those of the parasites. Contrary to this is the behavior of the aphi-

dophagous species of Coccinellidae. *Coccinella septempunctata* lays many eggs on clover and grass although no aphids are present on these plants (Banks, 1954*a*). *Adalia bipunctata* may lay eggs on branches of trees where no aphids are within easy reach of the young larvae (Hawkes, 1920). In such cases, the search for prey by the larvae is essential for survival of the species.

Searching Life of Larvae

Clustering and dispersal periods.—Eggs of *H. quinquesignata,* laid on alfalfa leaves or stems, were maintained at a constant temperature of 86° F (30° C), a relative humidity of 35 per cent, and without light. Observations were made at short intervals, one hour apart, when the time of hatching neared. Similar observations were made to determine the lengths of the clustering and the dispersal periods. Clustering time refers to the period the larvae spend on or near their egg shells from the time of hatching to the time the first larva disperses. Dispersal time refers to the length of the period from the time the first larva disperses until the dispersal of the last larva in the cluster for active searching.

TABLE 9

Duration of Clustering and Dispersal Periods of First Instar Larvae of *H. quinquesignata*

Number of larvae		Clustering period (hours)	Dispersal period (hours)
11		10.8	5.4
14		10.3	5.3
31		11.5	6.0
39		10.0	7.1
Mean..	24	10.6	6.0

The incubation period was about 2 to 3 days. The eggs remained yellow until several hours before eclosion, when the embryo's eyes began to show through the chorion as brown dots, its body darkened, and segmentation appeared gradually. The hatching larva was of a yellowish color, and it rested on the empty shell until its body darkened and hardened. Activities of larvae during the clustering period were as follows: After about one to two hours the larva began to move out of its egg shell and to search for food in the immediate vicinity. Unhatched eggs were the usual victims for these larvae. During the clustering period, larvae moved within the cluster, climbing on other larvae seeking for food. These movements were very restricted in the early part of the clustering period, but as time progressed searching became more thorough until all available eggs and hatching larvae were consumed. Then the larvae remained on or near the egg shells for the remainder of the clustering period. Search for food by larvae may be extended to neighboring egg clusters. Where there were still unhatched eggs, larvae remained longer than the clustering period shown in table 9, feeding on those eggs until all were consumed.

Fig. 5, A. The searching patterns of a *H. quinquesignata* first instar larva in the absence of food.

The length of this period depends also on temperature conditions. In one instance, larvae remained clustering for about 24 hours at 80° F (26.7° C). On the same basis this period probably would be shorter at higher temperatures.

Longevity of starved larvae.—The longevity of each instar was determined by caging larvae singly (size number 1 cage for first instar; number 2 for second instar, and number 3 for third and fourth instar larvae) and holding them without food until death. The larvae of second, third, and fourth instars had been fed well on *M. pisi* until they reached the required ages. Observations for the first instar were made on an hourly basis after the first deaths were noted. Observations for molting and mortality in the last three instars were based on 12-hour intervals. A larva was considered dead when all perceptible motions ceased. All cages were maintained at a constant temperature of 86° F (30° C), a relative humidity of 35 per cent, and without light.

As shown in table 10, searching life was longer in each stage than its preceding

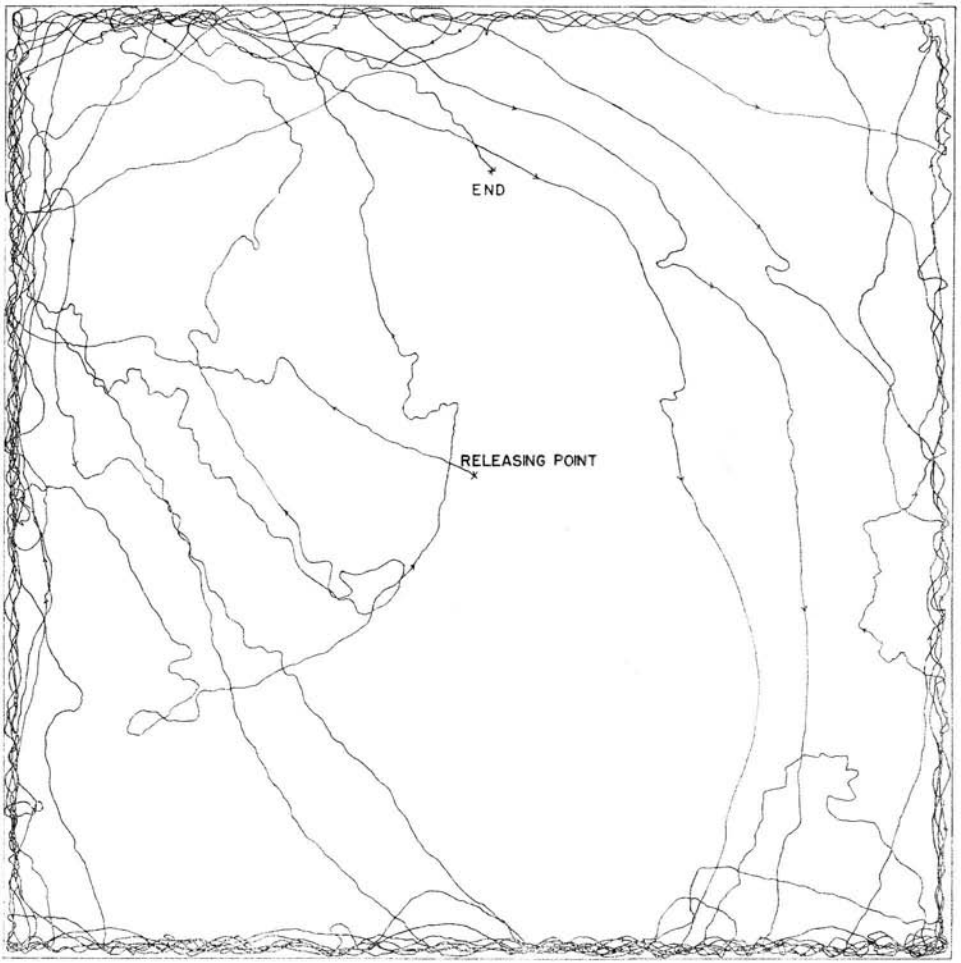

Fig. 5, B. The searching patterns of a *H. quinquesignata* fourth instar larva in the absence of food.

TABLE 10

SEARCHING LIFE OF STARVED LARVAE OF *H. quinquesignata*
(86° F, relative humidity 35 per cent, no light)

Instar	Number of larvae	Mean searching life (hours)
First	67	33.1[a]
Second	19	45.5
Third	15	48.8
Fourth	21	89.7

[a] Searching life of the first instar larvae does not include the clustering period. The total longevity was 46.7 hours.

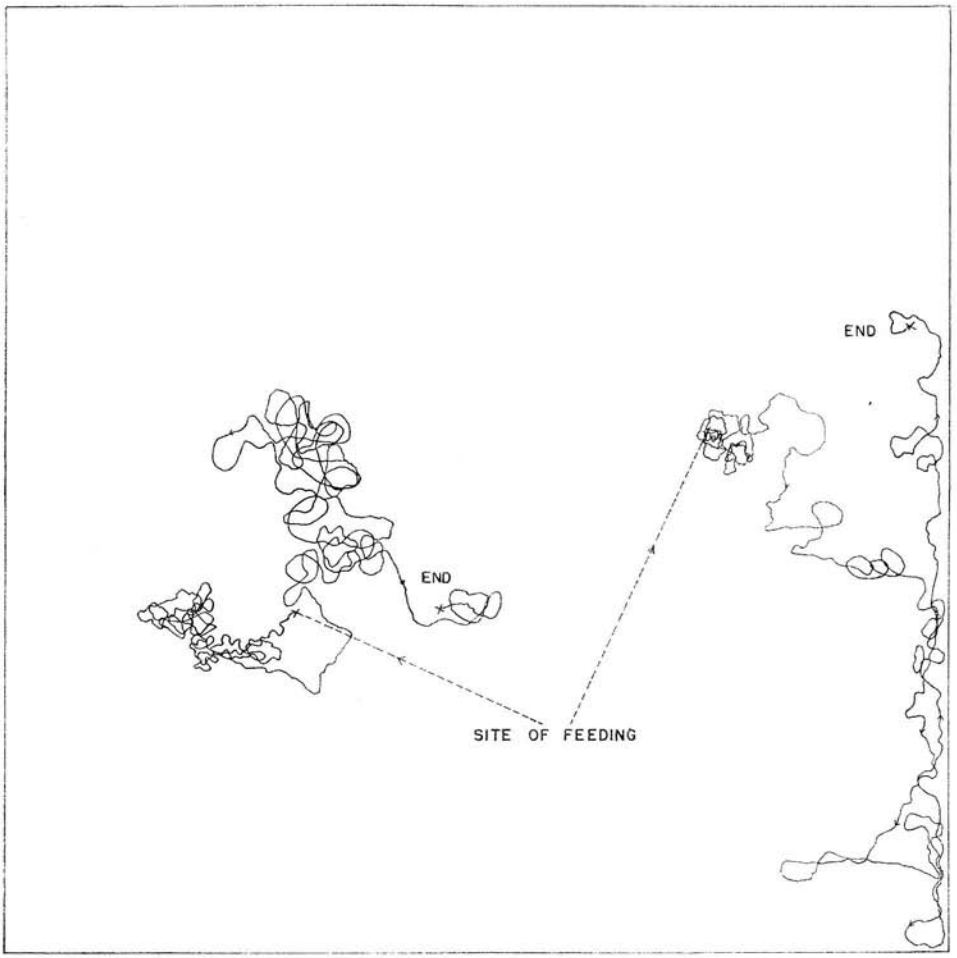

Fig. 6, A. The searching patterns of two *H. quinquesignata* first instar larvae immediately after finding and feeding on an aphid.

one. Larvae moved actively during most of their searching lives, and this activity continued as long as they could find enough food for growth and energy. But in the absence of hosts, the larval activities slowed down gradually until they died. During the last 12 hours before death they became completely inactive.

Another group of larvae, reared and maintained in a manner similar to that of the fourth instar in table 10, but at a temperature of 60° F (15.6° C) and relative humidity of 38 per cent, lived on the average 219.3 hours.

Searching Pattern and Behavior

On a large piece of plywood, a 24-inch-square searching universe was used. This field was surrounded by an electrically heated wire similar to that used by Flanders (1945) to confine larval activities to the universe, and was covered with buff drawing paper. The tested larva was released in about the center of the searching square, and its path was drawn by following it lightly with a pencil. Total

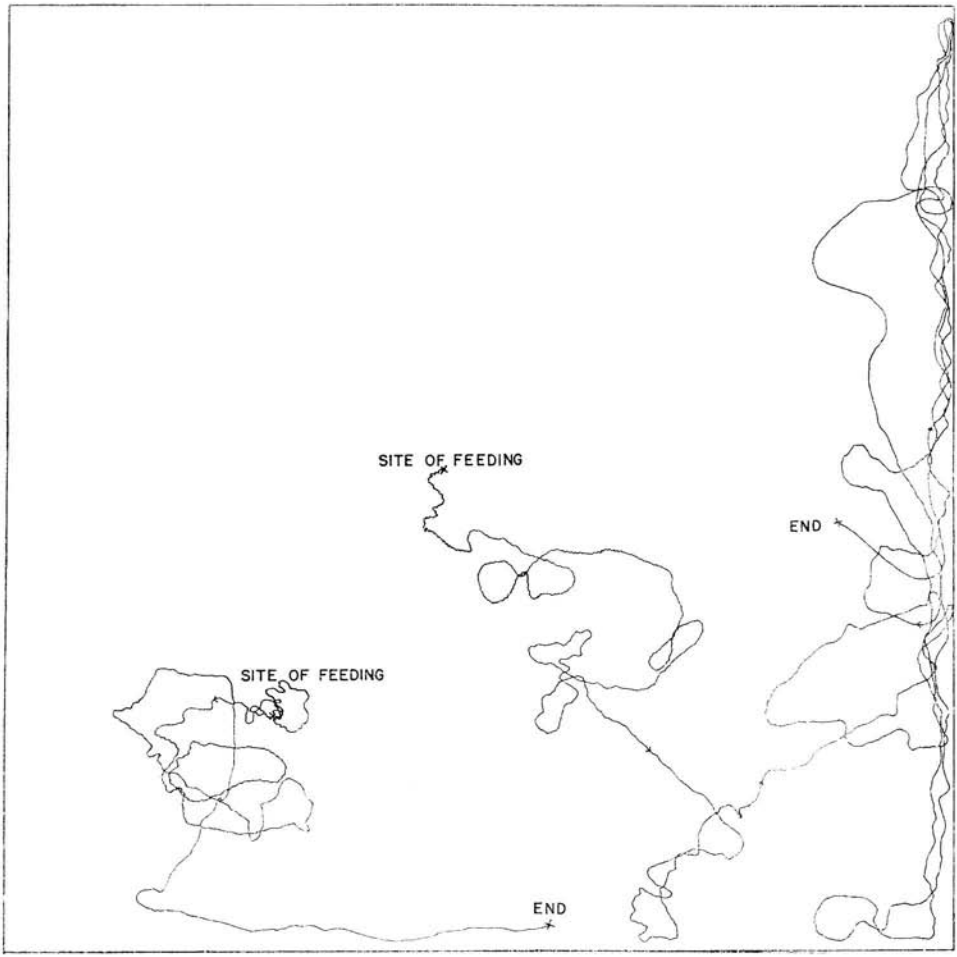

Fig. 6, B. The searching patterns of two *H. quinquesignata* fourth instar larvae immediately after finding and feeding on an aphid.

period for each test was 30 minutes. The searching universe was uniformly illuminated by a fluorescent light about 2 feet above. Intensity of the incident light on the field was 75 foot-candles. In order to study larval behavior after feeding on a host, the larva was given a small *M. pisi* to feed on. Each first instar larva was allowed to feed on an aphid in the searching field for 5 minutes, after which the aphids were removed. Each fourth instar larva was given an aphid which was completely consumed in about 3 minutes. Patterns of the larval movement were traced immediately after the feeding and continued for 10 minutes. The first instar larvae were 24 hours old and were unfed; their searching movements were conducted at a temperature of 78° F (25.6° C) and a relative humidity of 53 per cent. The fourth instar larvae were 48 hours old since their last ecdysis and were starved for 24 hours; their movements were studied at a temperature of 74° F (23.3° C) and a relative humidity of 62 per cent.

Searching of the first instar larva on a flat surface was of a random nature. The path was generally made in wide curves with frequent and abrupt changes in direction and rarely in straight lines. Paths crossed many times, making a network that covered the area searched. The searching path of the fourth instar larva was also of a random pattern. But this larva moved much faster than the younger one, with less frequent changes in directions, thus extending the lines (fig. 5). Both larvae showed a marked tendency to move along the hot wire barrier and tried many times to cross it, but they were unsuccessful. The searching larva frequently lifted its forelegs, prothorax, and head, as if trying to climb an object. Occasionally it stopped for a short time, then resumed activity. The total distance traveled by the first instar larva was 27.4 feet or a rate of 54.8 feet an hour, compared to 92.75 feet or 185.5 feet an hour by the fourth instar larva.

The path of the larvae after finding hosts was quite different from that noted earlier (fig. 6). The larvae here searched very slowly, moving their heads and bodies left and right in an arc covering a wider area than before feeding. They searched carefully for hosts in the immediate vicinity where the aphids had been found. After a short time the searching movements became faster and less twisted, forming lines approaching the normal pattern. There were no basic differences in the searching patterns of the younger and older larvae.

Phototropic Responses

In these experiments larvae of the same clusters were divided into two groups; one of them was tested when starved and the other when well fed. The first instar larvae were tested at the early clustering period, when 24 hours old, and again at 52 hours. Larvae at clustering stage were exposed to 60 foot-candle incident light at a temperature of 80.6° F (27° C) and a relative humidity of 45 per cent. Actively moving larvae of subsequent stages were tested by a different method. A searching field 24-inches square, covered with buff drawing paper and surrounded by a hot wire, was used. The field was divided, but not entirely separated, by a vertical board into two equal rectangle-shaped areas; the board left a space of ⅜ of an inch underneath. One side was uniformly illuminated by a fluorescent light about 2 feet above and gave an incident light of 75 foot-candles on the surface of the area. The other side was completely dark. The larvae had a free passage from one side to another through the space underneath the separating board (fig. 7). They were released on the borderline immediately under the dividing board, and their numbers on each side were counted at the end of 30-minute tests. The illuminated area was slightly warmer than the dark area. But to ascertain whether the insect response was a phototropic or a thermotropic one, the illuminated area was exposed to cool air by opening the room door in which these tests were carried out, and the dark area was heated by a hot plate. This test was conducted only with the first instar larvae. During observation times, except for the last test whose temperature conditions are indicated on the table of results (table 12), the temperature was 75.2 ± 1.8° F (23.0 ± 1.0° C) (measured by thermocouples), and the relative humidity was 60 per cent.

First instar larvae before dispersal from their egg shells were negatively phototropic. When exposed to light they crawled beneath the alfalfa leaves or to any

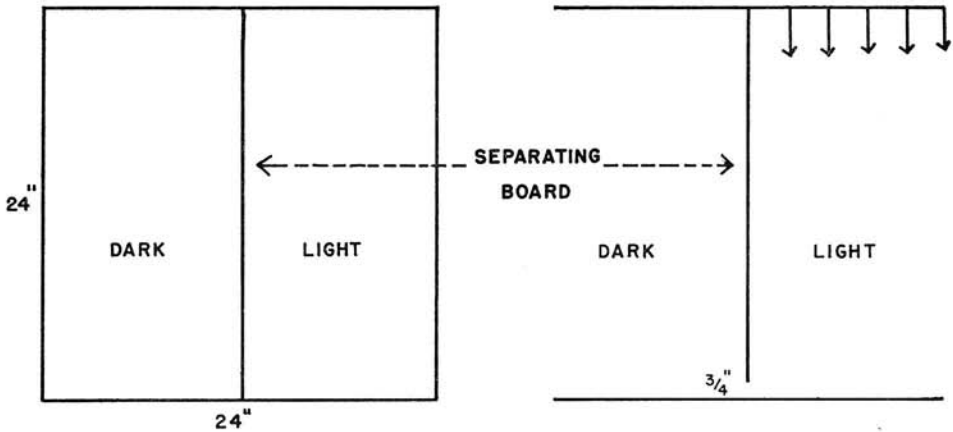

Fig. 7. The searching fields for the phototropic studies. *Left*, top view; *right*, side view.

shaded spots. This reaction was consistent every time the larvae were exposed to light, and also with other clusters of larvae observed incidental to other studies. All other stages of larvae also reacted negatively to light except first instar larvae at 24 hours old (table 11). Observations on molting and prepupating larvae indicate their negative responses to light. They usually seek such dark spots as inside curled alfalfa leaves or some refuge where light intensity is low.

Activities of larvae in the illuminated and dark fields were about the same except for the 24-hour-old first instar larvae which showed slightly higher activities in

TABLE 11

PHOTOTROPIC RESPONSES OF *H. quinquesignata* LARVAE UNDER STARVATION AND WELL-FED CONDITIONS

Number of larvae	Number of tests	Instar	Condition	Per cent of larvae responding to		Type of reaction
				Light	Dark	
		First instar				
150+	10+	Predispersal	Unfed	....	Higher	Negative
92	11	24-hour-old	Unfed	74.1	25.9	Positive
26	2		Well fed	84.3	15.7	
9	8	52-hour-old	Unfed	16.1	83.9	Negative
65	14	Second instar	Unfed	31.0	69.0	Negative
17	2		Well fed	38.3	61.7	
61	5	Third instar	Unfed	36.9	63.1	Negative
26	3		Well fed	29.4	70.6	
72	5	Fourth instar	Unfed	39.2	60.8	Negative
34	3		Well fed	39.3	60.7	

the illuminated field than in the dark one. As might be expected, they were more active when unfed than when well fed. Well-fed larvae usually showed greater activity in the illuminated than in the dark fields in the first parts of the tests. Eventually they became inactive just as those in the dark side. However, some of them continued their activity.

TABLE 12

PHOTOTROPIC RESPONSES OF 24-HOUR-OLD FIRST INSTAR UNFED LARVAE OF *H. quinquesignata* UNDER VARIOUS TEMPERATURE CONDITIONS

Per cent larvae responding to		Temperatures (F)	
Light	Dark	Light	Dark
88.3	11.7	72.5	72.5
93.3	6.7	82.5	80.0
82.4	17.6	81.5	79.5
68.8	31.2	79.5	77.5
100.0	0.0	64.0	76.0

Some of the active larvae moved back and forth from one side to another. As a result of these activities, the general pattern of reactions was reversed for the majority of the larvae on a few occasions and for short intervals.

The phototropic response of the young larvae was consistent regardless of the temperature conditions on both searching sides or the relative differences in temperature, as shown in table 12.

GEOTROPIC RESPONSES

Larvae were tested in an artificial field and on an alfalfa plant. The artificial field was made of two pieces of plywood connected to form two planes, vertical and horizontal (fig. 8), with a total area of 24 square inches. The area was covered with buff drawing paper and surrounded by a hot wire barrier. A larva was released in the center of the horizontal plane, and its path was traced with a

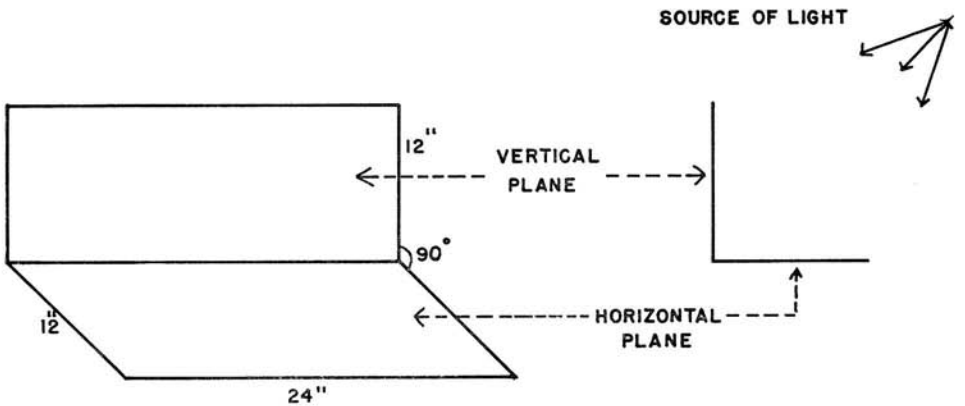

Fig. 8. The searching fields for the geotropic studies. *Left,* diagram; *right,* side view.

pencil for a total period of 30 minutes. The position of the light was adjusted to be equally distant from both the horizontal and the vertical planes and thus give a uniform illumination with incident light of 75 foot-candles on the searching surfaces. First and fourth instar larvae were tested. The former was tested at a temperature of 80° F (26.7° C) and a relative humidity of 30 per cent; the latter at a temperature of 80° F (26.7° C) and a relative humidity of 60 per cent. The first instar larva was 24 hours old and unfed. The fourth instar larva was 48 hours old since its last ecdysis and had been starved for the preceding 24 hours.

The alfalfa plant was about 12 inches high. The plant was divided into upper and lower parts at an arbitrary level of 6 inches. The foliage on both parts was approximately the same. Three larvae of each of the first and fourth instars were tested one at a time. The larvae were of the same ages and conditions as those tested in the artificial field. Each test began with the release of a larva at the mid-point of the stem, and the time the larva spent on each part of the plant was recorded for a total period of 30 minutes. These tests were conducted at a temperature of 73° F (22.8° C), a relative humidity of 60 per cent, and an intensity of incident light of 60 foot-candles.

In the first test, the insects searched both planes, the horizontal and the vertical, but spent a considerably longer time moving on the vertical plane than on the horizontal. Once again the larvae showed a preference to concentrate their activities along the edges near the hot wire (fig. 9), as demonstrated in figure 5.

Larval activities on the plant were a further demonstration of their negative geotropic responses. However, they were flexible in this behavior as in phototropism. The larvae searched both parts of the parts of the plant, the lower and the upper, but searched the upper part rather more thoroughly. The first instar larvae spent on the average 7.3 minutes on the lower and 22.7 minutes on the upper part of the plant, and the fourth instar larvae spent 6.7 minutes on the lower and 23.3 minutes on the upper part.

The larvae searched the plant in a random way. Their paths are similar to those shown on the flat surface. They were moving almost continuously with occasional halts, running along leaf edges, stems, and petioles which were visited for relatively longer times than other parts of the plant. Frequently they descended the plant and approached the soil, and in a few instances some crawled on the soil, then back up the plant. Some plant buds seemed to have been examined by the larvae rather carefully, and perhaps they obtained some kind of nutrition from them.

Host Finding

Host finding refers to the recognition, contact, and capture of a host by the predator. Starved larvae of the first and fourth instars were tested in a searching field consisting of a cylindrical paper carton, 3⅜ inches in diameter and 1½ inches high, covered with a Petri dish. Twenty cartons were used for the first instar larvae. Ten of them each contained 10 second instar *M. pisi*, and the other ten each contained 10 fourth instar *M. pisi*. To each carton one 24-hour-old first instar larva was introduced. The time required to capture the first aphid

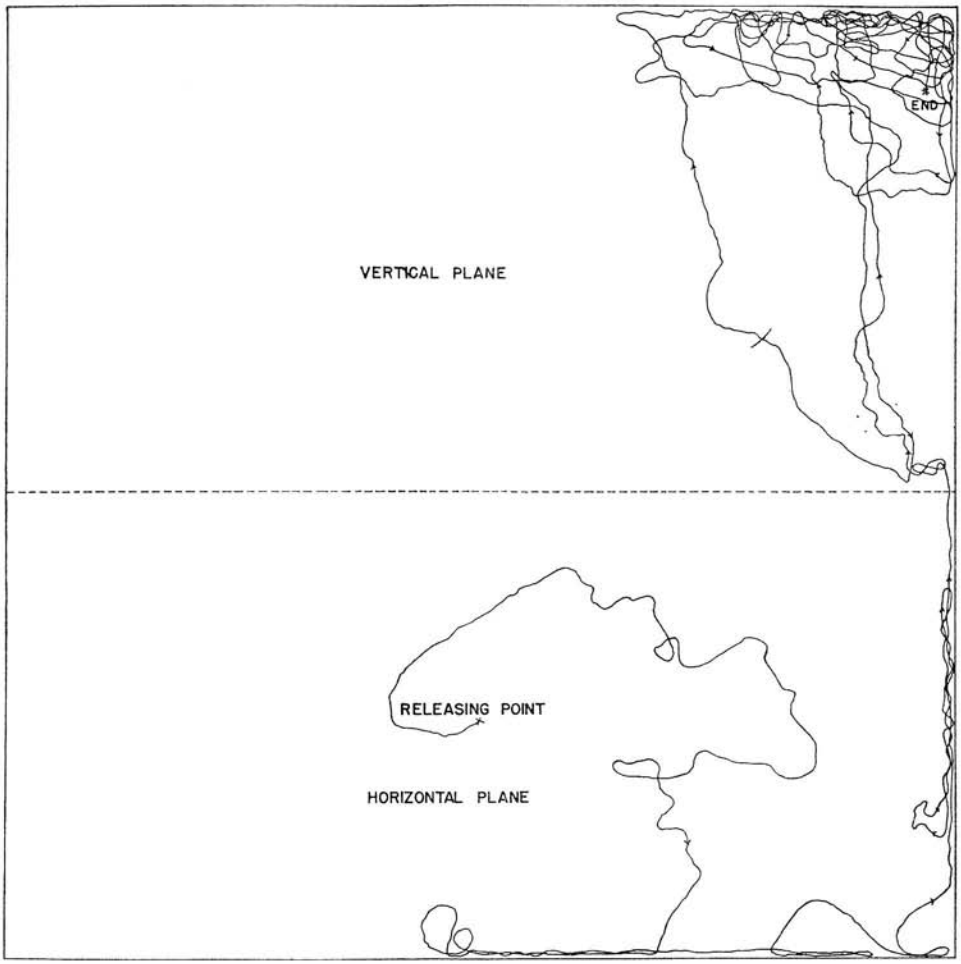

Fig. 9, A. The searching paths of a *H. quinquesignata* first instar larva on horizontal and vertical planes.

in each of these cartons was recorded. Observations were made at 5-minute intervals. Similar tests were carried out using fourth instar larvae, but because of the higher activity of these larvae, observations were made continuously.

The larvae seemed to have no power of perception to guide them toward their prey. They discovered the aphids only after physically contacting them. But the legs and the antennae of the pea aphid are long, and the aphid can detect the presence of the enemy in its neighborhood before the attack and escape. Usually, the larva first contacted aphid appendages onto which it clung by its mouthparts and forelegs. Then it moved gradually toward the prey's body. However, a larva which caught an aphid's appendages was still far from reaching the aphid's body. The aphid, with the larva clinging to its appendages, struggled to free itself and dragged the larva over the arena. The first instar larvae lost many such aphids, especially fourth instars. The forelegs of the first instar larva are much shorter

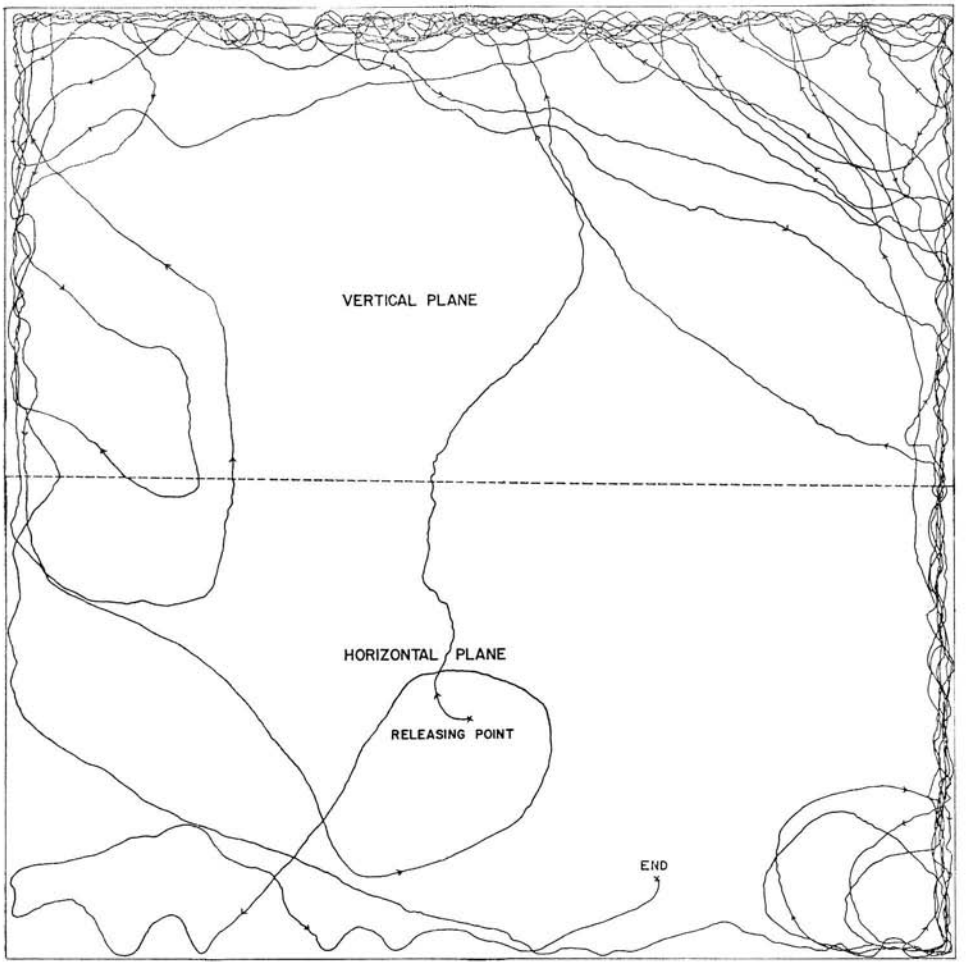

Fig. 9, B. The searching paths of a *H. quinquesignata* fourth instar larva in horizontal and vertical planes.

than the appendages of the aphid. Although its speed of movement is almost equal to that of the small aphids, it is a little slower than the larger aphids. Hence it must capture more appendages and crawl toward the body, using its forelegs to reach its prey. Once the larva caught the aphid's body, the capture was successful, for the aphid had a very small chance to escape. The larvae probably encountered as many fourth instar aphids as second instar. Only a few of these large aphids were captured by their appendages, and still fewer were finally killed. Fewer of the young aphids could free themselves from the first instar larvae. On the average, it took the first instar larva 48 minutes to capture a small aphid and more than 325 minutes to capture a large aphid.

Fourth instar larvae had no difficulty with the struggling aphids. These larvae have longer forelegs than the first instar larvae and grabbed the aphid's appendages and reached its body immediately after discovering it. They also could outrun

the aphids, and hardly an aphid, small or large, could escape once it was approached and recognized. On the average it took a fourth instar larva 6.9 minutes to capture a small aphid and 8.4 minutes to capture a large one.

In most cases when the aphids were crawling on the sides of the carton or on the underside of the Petri dish and were attacked by the larvae, they dropped to the floor of the carton and thus escaped the predator.

Discussion

At temperature of 86°F (30° C), the larvae of *H. quinquesignata* remain on the average 10.6 to 16.6 hours on or near their egg shells before dispersal. This period is longer at low than at high temperatures. It corresponds to 12 to 24 hours for larvae of *Coccinella septempunctata* Linnaeus, *Adalia bipunctata* (Linnaeus), and *Propylaea quatuordecimpunctata* (Linnaeus) (Banks, 1956), and about 12 hours for larvae of *Coccinella axiridis* Pallas (as *Ptychantis axiridis*) (Tan, 1934). No temperatures were given by these authors. During this clustering period the larvae are relatively inactive until their bodies harden and become strong enough to begin active searching for food. The larvae of *H. quinquesignata* may find some nourishment during the clustering period by feeding on unhatched or hatching eggs in their own or neighboring clusters. Some other species of Coccinellidae such as *Coccinella axiridis* have no desire to feed at this stage (Tan, 1934). The nourishment received by the larvae during this short period, even at the expense of others, is of great importance. Survival of the species depends to a large extent on the ability of these delicate first instar larvae to find food. Since the adult female may lay its eggs in places where no aphids are present, searching becomes essential for these larvae. Larvae which feed on eggs are better equipped to live longer and search farther than those which do not feed (Banks, 1954*b*).

The area searched by a natural enemy depends, in part, on the speed by which it moves, multiplied by its longevity. Since the speed at which first instar larvae move is slower (55 feet per hour) than that of fourth instar larvae (186 feet per hour), it seems probable that this speed increases progressively with the age of the larvae. The first instar larvae have a shorter longevity in the absence of food (table 10) than any of the subsequent instars. Their active searching life when caged at 86° F without food is little more than 20 hours (21.1) with about a half day inactive until death. This compares with 31 hours active and 25 inactive until death for the first instar larvae of *P. quatuordecimpunctata* (Banks, 1957). There is a slight difference between the longevity of the second and third instar larvae (45.5 and 48.8 hours respectively, table 10). The fourth instar larvae live considerably longer than any of the younger instars (89.7 hours). Therefore, as it immediately appears, the efficiency of searching is directly correlated with the age of the larvae.

Temperature has a significant influence on the longevity of the larvae in the absence of food. The prolongation of larval life by low temperature may not necessarily be advantageous to the survival of the larvae. Activities of the larvae at higher temperature may compensate for their shorter life.

In observations of the larval habits, it seemed that the larvae might be feed-

ing upon plant material. If this is true, it would aid their survival under conditions of low host densities.

The pattern of movement exhibited by the larva before finding a host enables it to search large areas effectively. The larva wasted some valuable time by searching rather thoroughly areas already searched and where aphids did not exist, and it left some other areas unvisited. Its behavior after finding the first host increases the chance of finding more hosts which may occur in the neighborhood of the first one. The turning movements of the predator after finding the first host are common to many other entomophagous insects, for example, larvae of *A. bipunctata* (Banks, 1957), larvae of *Stethorus picipes* Casey, *Conwentzia hageni* Banks, *Chrysopa plorabunda* Fitch (as *Chrysopa californica*) (Fleschner, 1950), and adult females of the chalcid *Trichogramma evansecens* Westwood (Laing, 1937). This type of movement is more advantageous to their natural enemies when the hosts are in colonies than when they are scattered (Banks, 1957). Once larvae find a colony of aphids they remain with it until that source of food is consumed or their development is completed.

The area effectively searched by a larva was measured by Fleschner (1950) on the basis of the width of the larval head and length of its track. Banks (1957) considered this area for the larvae of *C. septempunctata* to be a much wider path than the larval head, and it cannot be represented by a single track line. He found that these larvae, when searching, often stop, secure their abdomens to the surface, and move the rest of their bodies in an arc from side to side. Then they release their abdomens and move in a single direction. This action is repeated many times. Larvae of *H. quinquesignata,* searching for a host and before finding it, exhibit a path which can be represented by a narrow line equal in width to the distance between their forelegs. They do not attach their abdomens and move in an arc as do the larvae of *C. septempunctata,* but after finding a host the path becomes considerably wider. At that time the larval behavior and the width of the track approach those of *C. septempunctata.* The larva exhibits the side-to-side movement continuously without fixing its abdomen to the searching surface. If it does not find another host, it gradually changes its movements to the type usually exhibited before finding a host.

The apparent preference of the larvae to search in the vicinity of the hot wire barrier rather than in the center of the arena may have been owing to a positive thermotropic response, or possibly to a response similar to that noted on the plant. On the plant the larvae spent much of their time crawling at the edge of the leaves and on the petioles and stems.

The positive phototropic reaction of the first instar larvae in the early part of their searching life probably has some survival value. Larvae which hatch from egg clusters laid on or in the soil would be attracted to the light and hence climb up the plants where their hosts may occur. The reaction of molting and to a certain extent of prepupating larvae is of a protective nature. Larvae in these stages are open to attack by the active larvae (see Cannibalism, p. 213). The shaded hidden areas which they seek afford them favorable means of protection.

Tropic responses of an animal may vary with the species, its stage of development, and the existing environmental factors. Differences in specific tropic re-

sponses are already illustrated by the reactions of the larvae of *H. quinquesignata* and the species of Fleschner (1950) to tropic stimuli. Differences in the reactions of various developmental stages are shown in table 11, and also by phototropic reactions of larvae of *Coccinella undecimpunctata* Linnaeus. These larvae are negatively phototropic in their first and second instars and positive in fourth and possibly third instars (Hawkes, 1927). Temperature does not influence phototropic behavior of the first instar larvae of *H. quinquesignata* (table 12), at least in the temperatures studied. Potato beetles, when confined in a moist medium, reacted positively to light and negatively to gravity, but when the medium became dry, their reactions were reversed (Breitenbecher, 1918).

It is not absolutely necessary that the tropic responses of a natural enemy should correspond perfectly to those of its host. Naturally, a predator would encounter its host more readily if both reacted similarly to tropic stimuli than if they had different reactions. Citrus red mite, *Panonychus citri* (McGregor) (as *Paratetranychus citri*), is positively phototropic and negatively geotropic. Its predaceous larvae, *S. picipes,* have responses closely corresponding to those of the prey. Larvae of *C. plorabunda,* another predator of the mite, have a generally correlated geotropic response and a poorly correlated phototropic response to those of its prey. Larvae of *C. hageni,* a third predator of the citrus mite, have a closely correlated geotropic response and exactly opposite phototropic responses to those of the mite (Fleschner, 1950).

Freedom or flexibility of tropic limitations also influences efficient searching. Although the larvae of *H. quinquesignata* showed tropic preferences, they were of a flexible nature.

The behavior of various species of aphids when approached by a natural enemy adds further complication. Pea aphids, when approached by larvae, drop off the plant. Spotted alfalfa aphids are more stable on the plant. Early instars of both species adhere tenaciously to the plant. Also, both species are more stable when feeding than when they are not.

In conclusion, the question of which aphid species would be affected most by coccinellid larva predation depends on the relative tenacity of adherence of the aphids to the plant and the relative length of their appendages. Aphids more stable on the plants, such as the spotted alfalfa aphids, would be easier to capture than pea aphids. For the same reason, early instar and feeding aphids are more readily captured by their enemies than later instars and nonfeeding aphids. Spotted alfalfa aphids are easier to capture by the larvae than pea aphids for another reason than their tenacity in adherence to the plant. Their appendages are shorter than those of the pea aphids, and the larvae have less difficulty in seizing the struggling aphids. Also, the longer appendages of the pea aphids enable them to detect the approaching larvae and escape before they are attacked, whereas spotted alfalfa aphids may not be able to sense the presence of the larvae in their neighborhood until it is too late to escape.

It seems that there are no directional movements which lead *H. quinquesignata* larvae toward aphids, but chance plays the main role. The larvae find the aphids only after physical contacts are made. Similar behavior is manifested by the predaceous larvae, *S. picipes, C. hageni,* and *C. plorabunda* in finding their hosts,

the citrus red mite (Fleschner, 1950). Some other entomophagous insects possess powers of perception to recognize their hosts or the host's immediate environs, for example, *T. evanescens* perceives its hosts through olfaction (Laing, 1937). According to Laing, this parasite is attracted to the eggs by an odor left by the female moth, *Sitotroga cerealella* (Olivier). A physical contact sense is another effective perceptive quality by which the parasite recognizes the shape or mass of the eggs of the host. Laing also added that the physical contact sense guides the parasite of the leaf-mining larvae, *Phytomyza,* to track its host by following the mine.

First instar larvae are able to seize and feed on large aphids. However, their success in finding large aphids is very low compared to that of finding small aphids. The speed with which the fourth instar larvae captured their prey compared to that of the first instar larvae indicates the superiority of later instar over earlier instar larvae in finding host insects. On the basis of this data and the longevity in the absence of food, it seems that later instar larvae would be better able to survive under conditions of low host density. On the other hand (as shown in the section on Feeding Behavior and Capacity, p. 186), the first and second larval instars are of short duration, and larvae then require very small amounts of food.

CANNIBALISM

Cannibalism, a special case of predatism where individuals are devoured by their own kind, is a well-known phenomenon among some species of Coccinellidae (Marriner, 1926), including the phytophagous species, *Epilachna borealis* (Fabricius), in larval stages and the fungivorous species, *Thea vigintiduopunctata* Linnaeus, in both larval and adult stages (Balduf, 1935).

Although confinement or lack of favorable food leads to a higher degree of cannibalism, there is a certain degree of canibalistic mortality in the immature stages even when coccinellid populations are low or in the presence of abundant food and under natural conditions (Burgess, 1903; Hawkes, 1920; Watson and Thompson, 1933). Banks (1955), studying *Adalia bipunctata* (Linnaeus) and *Propylaea quatuordecimpunctata* (Linnaeus) on bean plants infested with *Aphis fabae* Scopoli, found that the destruction of coccinellid eggs by larvae was partly due to the scarcity of aphids but mainly to the relative location of aphids and eggs on the bean plants. The aphids infest the upper parts, and the egg cluster are on the lower parts of the plants. The larvae on their dispersal from the egg shells encounter egg clusters much more quickly than aphids. Banks also found that cannibalism occurred even on stems with relatively high populations of aphids. In his more recent work on *Coccinella septempunctata* Linnaeus, *A. bipunctata,* and *P. quatuordecimpunctata* on bean plants, Banks (1956) found that the percentage of fertile coccinellid eggs eaten by newly hatched larvae was higher in large egg clusters than in small ones. With *C. septempunctata* and *A. bipunctata,* which have large- to medium-sized egg clusters, about 10 to 12 per cent of the fertile eggs were eaten by larvae of the same cluster. For *P. quatuordecimpunctata,* where the egg clusters are small, this value was 6 per cent. In large clusters of eggs which have an extended hatching period, the first

hatched larvae attack unhatched eggs; smaller clusters hatch simultaneously. He also found that infertile eggs occur more commonly with *C. septempunctata* than with *P. 14-punctata* or *A. bipunctata*. They are all eaten by larvae of the same egg cluster.

Various coccinellid species exhibit different types of cannibalism. Hawkes (1920) noticed that adults of *A. bipunctata* and *C. septempunctata* fed on their own eggs under artificial conditions and also under natural conditions, but they never fed on larvae or pupae. *Coccinella divaricata distincta* Faldermann (as *Coccinella distincta*) behaved in the same manner in captivity (Donisthorpe, 1919). Hawkes (1927) stated that the young larvae of *Coccinella undecimpunctata* Linnaeus did not feed on the unhatched eggs of their own groups. Tseng and Tao (1936) reported that the beetles of *C. septempunctata, C. axiridis* Pallas, *Prophylaea japonica* Thunberg, *Hippodamia tredecimpunctata* (Linnaeus), and *Hyperaspis reppensis* Herbst resort to cannibalism by attacking their own eggs, larvae, and pupae when aphids become scarce.

Larvae of *A. bipunctata, C. septempunctata, C. quatuordecimpunctata* Linnaeus (as *C. variabilis*), and *Calvia quatuordecimguttata* (Linnaeus) (as *Halyzia quatuordecimguttata*) eat eggs, larvae, and pupae of their own species (Hawkes, 1920). Hawkes also found that some *A. bipunctata* eggs hatch earlier than others and that eggs which lag behind may be eaten by the newly hatched larvae. Mortality among larvae before dispersal from egg clusters rates about 25 per cent from this type of cannibalism.

Older larvae of *Leis conformis* (Boisduval) devour younger ones and sometimes larvae of their own size (Watson and Thompson, 1933). Larvae of *Adalia decimpunctata* (Linnaeus) (as *Coccinella dispar*) have been observed by Slater (1889) feeding on pupae of the same species on currant bushes where aphids were abundant. He did not observe this cannibalism in adult beetles.

Marriner (1926) reported that larvae of the two-spot lady beetle [= *Adalia bipunctata* (Linnaeus)] in England feed on the egg shells after hatching, then on larvae of the same cluster before dispersal. According to Hawkes (1927), larvae of *C. undecimpunctata* did not feed on egg shells or unhatched eggs. There was no cannibalism in the early stages such as occurs with *A. bipunctata*.

Larvae that feed cannibalistically develop in a shorter time than do other members of their groups. But later these larvae may themselves become prey to larvae which lag behind in development. Cannibalistic larvae reach ecdysis periods earlier than others. For the purpose of molting, larvae attach themselves to an object by their caudal ends and become motionless. At this stage they are very easy prey for active larvae. This dangerous period occurs four times, once at the end of each larval instar (Hawkes, 1920).

The nourishment obtained through cannibalism is apparently not a perfect one, at least in some known cases. Tan (1934) had fed larvae of *Coccinella axiridis* at early stages on unhatched eggs, and at later stages on young larvae of the same species. The cannibalistic larvae went through ecdyses and pupation regularly but with a very high rate of mortality (90 per cent).

As stated earlier by many authors, cannibalism may result in a high mortality among species which practice this type of feeding. Nevertheless, it is considered

of great biological significance in preserving the species. The larvae, under stress of unfavorable circumstances, cannot fly to more favorable locations, nor can they remain for a long time without food, as the adults do (Hawkes, 1920). Females of *A. bipunctata* may lay eggs on branches of trees where there are no aphids within easy reach of young larvae which cannot travel far in search of food. The capacity of these larvae to eat eggs and other larvae is of considerable survival value. Banks (1954*b*) stated that the larvae which fed on unhatched eggs lived longer and traveled farther than those which did not feed. The larvae which were fed one egg each lived on the average twice as long as did the unfed larvae. Their longevity would be expected to be even greater if they were fed two or three eggs. Marriner (1926) stated that the availability of aphids for the newly hatched larvae cannot be predicted by the female coccinellid at the time of egg laying. He believes that the nourishment obtained by these weak larvae from eggs of the same clusters is essential and comparable to the feeding of the young plant on the seed's endosperm until it can depend on itself.

Materials and Methods

The experiments were designed to study degrees and rates of cannibalism among larvae of the same stage in the four larval stages and of some combinations of immature stages. Among the latter were experiments on cannibalism of newly hatched larvae on eggs of their own egg clusters, of third instar on fourth instar larvae, of fourth instar larvae on prepupae, and of fourth instar larvae on pupae.

During these experimental periods, the cages were held in a temperature cabinet at $86 \pm 1.8°$ F ($30 \pm 1.0°$ C) with a relative humidity of 30 per cent and no light. At times of observations, the cages were kept at a temperature of $79.3 \pm 1.6°$ F ($26.3 \pm 0.9°$ C), a relative humidity of 40 per cent, and an incident light of about 60 foot-candles from a combination of an incandescent table lamp and fluorescent ceiling lights.

For the experiment on cannibalism of young larvae on eggs, egg masses were obtained from the stock colony. These eggs were laid largely on alfalfa leaves and occasionally on stems in the colony cages. The clusters were maintained undisturbed in paper cartons covered with Petri dishes and incubated in a temperature cabinet with the conditions mentioned above.

In cases of larval cannibalism on others of their own stage, three larvae of the same age were placed together in each cage. For the other tests, cannibalism of younger larvae on older ones, of fourth instar larvae on prepupae, and of fourth instar larvae on pupae, there were two individuals in a cage, one each of the immature stages used in combination. Ten trials were made of each combination except the first one—cannibalism of young larvae on eggs.

For cannibalism in the first stage, 24-hour-old unfed first instar larvae were maintained in size number 2 cages. One hour after establishing the experiment, one adult apterous spotted alfalfa aphid was introduced into each cage. This was enough to supply nourishment to prolong the longevity of the weak, short-lived larvae, and yet not sufficient to complete the development of the first stage. Observations were made after 1, 2, and 12 hours.

For tests of cannibalism of larvae by others of the same stage, partly starved

insects were used. The second and third instar larvae averaged 12 hours old, and size number 3 cages were used; the fourth instar larvae averaged 36 hours old, and were maintained in size 4 cages. Ten larvae of the same age and source as those used in the last three tests were caged singly, held under the same conditions, and used as longevity controls for their corresponding groups. Observations were made at the first hour and then at 12-hour intervals from the time the tests were established. To avoid including larvae which died from natural causes and then were fed to larvae which were later killed, only results of the first 12-hour period were used. During this period there was no natural mortality in the check group (table 15).

A combination of a hungry third instar and a well-fed fourth instar larva was placed in a number 3 cage. The purpose of this test was to study cannibalism of younger larvae on older ones. The fourth instar larvae were maintained in this nonfeeding condition as much as possible for the duration of the test period by taking them out of their cages and feeding them on pea aphids once every three hours. Other third instar larvae were given no aphids and were maintained at this state of hunger during the period. Observations were made at 3-hour intervals for a total period of 12 hours.

Each of ten mature larvae in the prepupal stage was maintained in number 4 cage. Another group of ten mature larvae each pupated in similar cages. To each of these cages one partly starved fourth instar larva was introduced, and observations were made at 12-hour intervals. These two tests continued until the larvae either succeeded in feeding on their prepupal or pupal mates or died. The larvae used in these tests were not used again in any tests, except that some were used as prey in their prepupal or pupal stages. There was some indication that larvae previously involved in cannibalistic feeding attacked others more readily than those that had not fed through cannibalism.

Results

Cannibalism of newly hatched larvae on eggs.—The results in table 13 indicate that when the hatching period was less than one hour there was no loss in hatchable eggs. Egg clusters with hatching periods of one hour or more had various degrees of egg destruction which ranged from 0.0 to 33.3 per cent. The newly hatched larvae did not begin to feed until they were at least one hour old. The hatching larvae gradually pulled themselves upward from their egg shells, but remained attached by their caudal ends to the inside of the shells for about one to two hours. During this period their color changed from yellow to black, and their bodies hardened. As early as one hour after hatching, some larvae moved out of the egg shells and began feeding on neighboring unhatched eggs.

Hatching rates (table 14) indicate that most of the eggs in a cluster hatched within a short time but the remaining few required considerably longer. The destroyed eggs in table 13 were among those that were delayed in hatching. The total percentage of eaten hatchable eggs was 7.8 per cent. On the average, there were 6.6 feeding larvae to each eaten egg, including both hatchable and nonhatchable. In other words, each feeding larva consumed on an average 0.15 of an egg.

TABLE 13

CANNIBALISM OF EGGS BY NEWLY HATCHED *H. quinquesignata* LARVAE OF SAME EGG CLUSTER

Hatching period (minutes)[a]	Number of hatched eggs	Nonhatchable eggs	Hatchable eggs destroyed	
			Number	Per cent
45	5	0	0	0
45	14	0	0	0
50	8	0	0	0
50	15	2	0	0
55	7	2	0	0
60	14	1	1	6.7
70	11	0	0	0
75	31	4	0	0
88	39	0	3	7.2
115	22	0	3	12.0
120	11	1	0	0
120	19	0	2	9.5
165	13	0	3	18.7
175	6	1	3	33.3
195	11	4	4	26.7

[a] The term "hatching period" refers to the length of the period from when the first larva begins to hatch to the complete hatching of the last larva of the same cluster.

TABLE 14

HATCHING RATES OF *H. quinquesignata* EGGS

Number of hatchable eggs in the cluster	Eggs hatched at[a]						Number of nonhatchable eggs in the cluster
	0–60 min.	61–90 min.	121–135 min.	166–180 min.	196–210 min.	286–300 min.	
7	6	0	0	1	0	0	0
8	4	2	1	0	0	1	4
10	9	0	0	0	1	0	2

[a] Larvae hatched beyond the first hour of hatching were protected from the previously hatched larvae by removal of the latter after hatching.

Cannibalism in the first stage.—The larvae during the first hour of confinement moved about rapidly with occasional unsuccessful attempts to capture prey. When an aphid was introduced, all the larvae fed on it simultaneously without any antagonism toward each other. However, in three out of ten instances only two larvae found and captured the aphid while the third larva was still searching for food. In each of these instances, the wandering larva attacked one of the feeding larvae. The larvae which were attacked on their backs and legs could easily release themselves and repulse the offenders. Those which were attacked on their abdomens had to struggle very hard to free themselves from the cannibalistic larvae, which had a strong hold on the soft abdomen.

In general, the larvae defended themselves by whipping offenders with their caudal ends, by retaliatory biting, or by merely sitting with heads bent down

slightly as if they were trying to protect the most vulnerable part of their bodies—the venter. The hard spiny dorsum was unacceptable, but the venter was quite acceptable and vulnerable to cannibalistic attacks. When upright, even the weak larvae, newly hatched or dying, were not attacked by hungry larvae. Some larvae died, apparently from natural causes, but were not eaten by the starving larvae.

Cannibalism in the last three larval stages.—In each of these stages, the larvae were more pugnacious as well as stronger in repulsing attacks of others than in earlier stages. The larvae moved rapidly about, antagonizing each other, and fighting off offenders in the same manner described for the first instar larvae. Prey-sharing was also a common phenomenon in these three stages. One fourth

TABLE 15

CANNIBALISM BY THE LARVAL INSTARS OF *H. quinquesignata* AT THE END OF 12-HOUR EXPOSURE PERIOD AND THE EFFECT ON LONGEVITY

Instar confined	Dead larvae in test group		Longevity of check larvae (hours)[a]		Longevity of cannibalistic larvae (hours)	Average time required to capture prey (hours)
	Number out of 20 total potential prey	Per cent	Range	Mean		
First	7	35	16–31	22.7	....	12.0
Second	20	100	24–36	30.0	33.6	11.4
Third	20	100	24–48	33.6	44.4	8.1
Fourth	18	90	24–60	43.2	76.8	8.3

[a] Longevity of check group of the first instar larvae were taken from table 10.

instar larva was seen to make a sudden attack and inflict a serious wound on another larva. The prey was able to free itself for a short time, but the wound induced a persistent chasing and attack by another larva, and the wounded individual soon succumbed. Many of the victims in this experiment were completely consumed in contrast to the amounts eaten in the preceding stages. The mortality of the potential prey in the second and third stages was slightly higher than in the fourth stage. The average length of time required to capture the prey followed the same pattern of the mortality (dead larvae in test group) in table 15, but inversely. It required a longer time in the early stages than in the later stages, with a slight reversal in the fourth stage.

The longevity of the cannibalistic larvae was always higher than that of their corresponding check groups. The differences between the longevities of these two groups, the cannibalistic larvae of a stage and the check larvae of the same stage, were greater at each stage than its preceding one (table 15).

Cannibalism of younger larvae on older ones.—The hungry third instar larvae did not seem able to capture any of their older mates. Their attempts were effectively repulsed by the larger and stronger larvae. They were inclined to avoid each other with frequent antagonistic reactions. At the end of the 12-hour period there was no mortality in the fourth stage (table 16), but two younger larvae were killed by the older ones.

Cannibalism on the prepupae.—The degree and rate of prepupal mortality

(table 16) indicate that the prepupae were quite acceptable and vulnerable to larval attacks. They have distended bodies and tender integuments. Immediately after the puncturing of the prepupal integument by the larvae, body fluids poured out. This made the prey more acceptable to the hungry larvae. The only defensive reaction of the prepupae was a sudden rocking movement of their bodies. This movement frightened some larvae but only temporarily, and the presistent larvae eventually succeeded in feeding on the prepupae. The bodies of the prey were largely consumed except such heavily sclerotized parts as the heads and some parts of the thorax and legs.

In the stock colony this type of cannibalism was a serious factor in prepupal mortality. This was especially serious at times when aphids were not available and when larvae were reared in small paper cartons with no hiding places. For

TABLE 16

CANNIBALISM OF THREE COMBINATIONS OF IMMATURE STAGES OF *H. quinquesignata*

Stage of hungry larvae	Stage exposed to cannibalism	Number cannibalized out of ten potential prey				Per cent killed (48 hrs.)
		0-12 hours	13-24 hours	25-36 hours	37-48 hours	
Third instar.....	Fourth larval instar[a]	0	..	..	..	0
Fourth instar.....	Prepupa.....	7	3	..	..	100
Fourth instar.....	Pupa.....	1	1	0	2	40

[a] The larvae in this group were well-fed individuals.

prepupation, mature larvae seek dark, hidden sites, as inside curled or underneath alfalfa leaves, away from the main population of the wandering larvae. Thus some of them escape cannibalism.

Cannibalism on the pupae.—Some of the larvae showed only casual interest in the pupae until they died. Others attempted to feed on the pupae but unsuccessfully. Four larvae out of ten, however, could eat their way into the well-protected pupae. The pupae were attached to the cage surface, and their abdomens were well concealed and protected. A few larvae were able to insert their heads underneath the pupae and reach the soft parts. Shortly after they began feeding, the pupae loosened and raised their bodies, exposing their abdomens and making them accessible to the larvae. The pupae which were not eaten by the larvae developed into apparently normal adults.

DISCUSSION

There seems to be no correlation between the size of the egg cluster and the degree of cannibalism on eggs of *H. quinquesignata* such as that reported by Banks (1956) for *Coccinella septempunctata, Adalia bipunctata,* and *Prophylaea 14-punctata.* But there is a correlation between the length of the hatching period and the degree of egg destruction, which agrees with his results. The longer the hatching of individual eggs in a cluster is delayed, the higher is the probability of their being destroyed by larvae which hatch earlier. This correlation between the hatching period of the eggs and the degree of cannibalism is not perfect.

However, the discrepancies may have been caused by other factors. Among these, first, only a few larvae begin to feed when they are one hour old. After this period, the number of feeding larvae gradually increases, but the rate of this increase is slow in some groups and rapid in others. Second, the relative position of the late-hatching eggs to the other eggs in the cluster contributes to the egg survival. Eggs which are separated from the feeding larvae by nonfeeding younger larvae have a better chance to hatch than those in close contact with the feeding larvae. Third, the larvae feed singly or in groups. Several larvae feeding together on one egg results in lower egg mortality than when larvae feed singly. Fourth, if the feeding larvae attack the nonhatchable eggs when available, the late-hatching eggs may escape cannibalism. The nonhatchable eggs seem to occur at random in egg clusters regardless of the sizes or sources of the clusters.

Cannibalism on eggs by larvae from other clusters was not studied. The total destruction of eggs by larvae of the same cluster and by those of other clusters and other instars would be higher than that obtained here.

The larvae fed little or not at all on the egg shells. This is in contrast to the larvae of *A. bipunctata* (Marriner, 1926). The degree of cannibalism on eggs by the young larvae of *H. quinquesignata* would be lower had these larvae the capacity to feed on their empty egg shells.

A capacity for cannibalism is present in all larval instars. The degree of cannibalism of each instar is modified by various factors. In confinement it is determined by the pugnacity and aggressiveness of the cannibalistic larvae and their ability to feed through the hard integument of the larvae, as against the ability of the prey to avoid cannibalism by retaliatory biting, whipping the cannibalistic larvae by the caudal ends, or sitting firmly in the cage. Other factors which play a role in nature will be discussed below.

The mouthparts of the first instar larvae are weak. Feeding in this stage is accomplished by piercing the soft parts of the prey's body, then sucking juices from these wounds. There is very little chewing. This type of feeding gradually changes to chewing as the larva develops. This fact is supported by the gain in longevity of the larvae resulting from cannibalistic feeding, which was lower in early instars than in successive later ones (table 15). Pugnacity and aggressiveness of the larvae and also their power to fight off cannibalistic larvae are at the lowest level in the first instar and increase rapidly with the age of the larvae, reaching the highest level at the fourth instar.

The limited feeding capacity of the first instar larvae is probably responsible for the lower degree of cannibalism in this stage. Many larvae which died naturally were not attacked by the hungry larvae in the same cages. In the second and third instars the ability of the larvae to eat others seemed to be relatively more effective than their ability to escape cannibalism. This is evidenced by the results obtained for those two stages (table 15). As might be expected, it took a longer time to capture a prey in the second instar than it did in the third instar. Results of the fourth instar larvae indicate a slight reversal in favor of prey survival. The larvae then were most efficient in defending themselves from approaching enemies. The result demonstrated the ability of well-fed fourth instar larvae to avoid cannibalism when exposed to hungry third instar larvae (table 16).

Cannibalism of older larvae on younger ones was not studied here. But it can be concluded that there would be a higher degree of cannibalism on younger larvae than on larvae of the same stage.

The prepupae were quite easy prey for hungry larvae. Their ability to avoid cannibalism in confinement is limited to rocking movements of their bodies. This is very inadequate against the aggressiveness and feeding capacity of the fourth instar larvae (table 16). Hence mortality in this stage was very high. This is true in confinement. In paper cartons covered with Petri dishes, where larvae of the stock colony were reared, most of the prepupae were eaten by the active larvae at times when sufficient aphids were not available. Comparable to this mortality is that of the larvae during ecdysis periods (Hawkes, 1920). The larvae at these times secure themselves to an object and become motionless just as do the prepupae. High mortality of these helpless larvae resulted from feeding by the active larvae.

The behavior of larvae toward pupae indicates that the pupae are not readily acceptable to the larvae and that they are resistant to larval attacks. The mechanism of this resistance apparently lies in their protective integument.

Projection of these laboratory results to natural conditions will modify some features. In all cases, the degree of mortality caused by cannibalism is greatly influenced by the relative population densities of the coccinellid larvae and the host insects. The degree of egg destruction depends on the relative location of the aphids and the egg masses on the host plants at the time of hatching. If the host insects are readily available to the feeding larvae there should be a lower degree of cannibalism on eggs than if host insects are scarce. The factors which modify cannibalism on larvae in the field are searching capacity and the ability of the prey to run away from their enemies. The latter leads to a lower degree of mortality in the field than in confinement. The younger larvae are subject to a higher degree of cannibalism by older larvae than by larvae of their own stage. Also, on the other hand, some of the older larvae fall victims at molting periods to younger active larvae. This mortality is probably not serious. Two factors reduce the degree of mortality of the molting and prepupating insects. Larvae going through molting and prepupating processes prefer hidden and dark sites and thus avoid cannibalism. Also, the brevity of these two substages reduces the exposure of these susceptible insects to their enemies.

Feeding of the coccinellid larvae on immature stages of the same species has a significant role in preserving the race. Availability of host insects, mainly aphids, varies from season to season. In alfalfa fields, cutting the hay results in a sharp reduction in the population density of aphids, but the population density of coccinellid insects increases relatively. Treatment of the fields with selective chemicals against aphids may leave the predators without aphids for periods of time ranging from a few days to a few weeks. The onset of unfavorable weather conditions for the aphids also reduces their populations and makes them less available to their predators. In these circumstances adult coccinellids fly to more favorable locations or remain alive without food longer than the larvae can. The larvae then derive their nourishment either from other host insects or from their own kind. Larvae in a situation with no food and without the ability to travel to another more favorable area would die had they not this cannibalistic faculty.

Some larvae in an advanced fourth instar may pupate under such adverse conditions. The faculty of the larvae to feed cannibalistically enables some of them to prolong their lives (table 15) until the situation changes and becomes favorable or to complete their development and fly to another area.

SUMMARY

Female beetles of *Hippodamia quinquesignata* usually lay their eggs in clusters. In cages they laid them on leaves and stems of alfalfa plants and cuttings and sometimes on the sides of the cages (on the glass or on the wood). The incubation period of the eggs is 2 to 3 days at 86° F. The hatching period of an egg cluster ranges from about half an hour to several hours; its length is independent of the size of the egg cluster. After hatching and at 86° F, larvae remain near their egg shells 10.6 to 16.6 hours. This time before dispersal—the clustering period—is shorter at high than at low temperatures. During the clustering period larvae may feed on eggs of their own clusters or of those in the immediate neighborhood. On an average, each larva at this stage eats 0.15 of a coccinellid egg, either hatchable or nonhatchable. The longer the hatching period of an egg cluster is delayed, the greater is the probability of its being destroyed by larvae which hatched earlier. As a result of this cannibalistic feeding, 7.8 per cent of the hatchable eggs are destroyed by larvae of the same cluster. Undoubtedly, this loss is higher when eggs are exposed to attack by larvae from other groups and other stages, and especially at times of relative scarcity of host insects.

The cannibalistic behavior of larvae at the clustering stage has a survival value even at the expense of some eggs. Larvae often hatch where there are no aphids in the vicinity and they have to search, sometimes at long distances, before finding food. Unfed first instar larvae have a short searching life and travel a short distance, but fed larvae continue searching and growing as long as they find enough food.

After the clustering period, some larvae begin to disperse, searching for food. If larvae cannot find any kind of food they continue searching incessantly until about the last 12 hours of their lives, when they become inactive until death. The average longevity of unfed caged larvae at 86° F is 46.7 hours for the first instar (first 10.6 to 16.6 hours is the clustering period), 45.5 for the second instar, 48.8 for the third instar, and 89.7 hours for the fourth instar larvae.

In their searching, larvae exhibit two kinds of movements; random cursory movements covering large areas searching for suitable places where their host insects may occur, and slow, winding and more detailed movements (after finding and consuming a host) searching for more host insects in places where they are likely to occur. These winding movements aid the larva to find hosts having a contagious distribution more easily than those randomly distributed. Aphids—the main host insects—generally occur in groups.

Finding a host insect by a larva seems to be a matter of chance. There is no apparent directional movements which guide larvae toward aphids; they perceive their host insects only after physical contacts are made. This is no handicap for a predator with a searching capacity as efficient as that of *H. quinquesignata*. Faculties which make up for lack of perception other than the contact sense are

speed and persistence of searching, flexibility of tropic behaviors, and types of searching movements which make searching more efficient.

Larvae have the ability to seize and feed on aphids many times their size. Success of younger larvae in this pursuit, however, is limited. Morphology and behavior of aphids approached by larvae influence host finding. Host insects with long appendages, legs, and antennae can detect the presence of a larva in the vicinity before capture and thus have a chance to escape, whereas short-appendaged host insects cannot sense the presence of the enemy until it is too late. Larvae usually capture aphids first by their appendages, then move gradually toward the prey's body. In the meantime, the aphid struggles with the larvae and may free itself. Long-appendaged host insects have a better chance than short-appendaged insects to release themselves in struggling with larvae. The stability and tenacity of host insects to the plants are other important factors in host finding. More tenacious insects are easier to capture than nonstable, excitable insects. This property varies with the insect species (*T. maculata* is more stable and tenacious than *M. pisi*), with the stage of development (younger instar aphids are more tenacious than later instars), and with feeding activities (feeding aphids are more tenacious than nonfeeding aphids). According to these criteria, *M. pisi* is harder to capture (has long appendages, is less tenacious, and is excited by any disturbance) by natural enemies than *T. maculata*. Under laboratory experiments in cages, larvae of *H. quinquesignata* showed a slight preference for *M. pisi* over *T. maculata*. In nature, this apparent preference may be modified or even reversed for *T. maculata*.

Normal feeding activity and probably other activities also are restricted to temperatures from slightly below 60° to slightly below 99° F. The highest lethal low temperature is about 50° F, and the lowest lethal high temperature is about 99° F.

Young larvae (first and early second instars) feed mainly by sucking body fluids of the host insect, leaving only the shriveled skeleton. Later instar larvae feed on the fluids of the host insect and the skeleton as well. They usually exhibit what is called external digestion, similar to that of many other predaceous insects.

Feeding rates of coccinellid larvae are influenced by many factors. Among these are insect species, stage of development, temperature conditions, population density of the host insect, sex, and history of larvae in relation to amounts of food they previously consumed (starvation effect). Laboratory experiments of the present investigation and of those reported in literature indicate that larvae of various species of Coccinellidae, even closely related species, have different rates of feeding. In order to attach biological and ecological significance to feeding capacity it must be qualified by other attributes, among which are host specificity, tolerance limits to environmental conditions (distribution), searching capacity, feeding capacity of the adults, fecundity, fertility and natural enemies. Although the feeding capacity of *H. quinguesignata* larvae on aphids seemed, under laboratory conditions, lower and their growth rate slower than many other coccinellid species, this species is considered a much more important aphidophagous species in California under natural conditions than many of the others. Those other species are not as abundant, not as widely spread, or are not aphid-specialized feeders.

The feeding capacity increases progressively with the age of the larvae. Later instars are voracious, kill large numbers of aphids, and consume most of them, whereas younger larvae kill fewer aphids and consume them only partly. Temperature affects the feeding capacity of the various instars. The lowest feeding rate is at 60° F, and the rate increases up to 86° F, then drops at 90° F. The growth rates at various temperatures correspond to a large extent with the feeding rates at those temperatures, leading to the inference that slow growth rate may be caused by partial starvation. The harmful effects of extreme temperatures may result from a complete starvation. Temperature fluctuation may stimulate feeding as evidenced by the reaction of larvae of other species of Coccinellidae.

The larvae act on the host population in a density-dependent manner. Larvae, at high host density, feed up to the maximum capacity, develop into large individuals which require and are capable of consuming large numbers of aphids, and develop in a very short time. Where host density is low, larvae are less effective in controlling aphids through the adverse effects of starvation. Under those conditions larvae developed into smaller individuals of low feeding capacity and have a prolonged development with a high rate of mortality.

The feeding capacity of the female larva is higher than that of the male larva at temperature conditions up to the optimum (about 86° F). When temperature is higher (90° F) the male larva achieves a higher feeding capacity than the female. In consequence, the larvae of higher feeding capacity are more effective in combating aphids at high host population density.

Finally, larvae reared on an abundance of aphids grow large and consume large numbers of aphids, whereas starved larvae or larvae reared on a low number of aphids develop into small larvae with a lower feeding capacity. The larvae have a very broad range of feeding rates. Although some larvae completed development on as few as 1.2 aphids (second instar *M. pisi*) a day, others ate as many as 31.7 aphids a day at 86° F. This broad range in feeding rates and well-developed tolerance to starvation characterize an effective entomophagous insect species.

At times when the preferred host insects are scarce, larvae resort to other available sources of food. These may be other species of aphids, leafhoppers, psyllids; eggs or young larvae of such insects as the asparagus beetle, the Mexican bean beetle, and some lepidopterous insects; a nutrient obtained from a plant source; or members of the same species (cannibalism). In the latter case, coccinellid eggs and young, molting, and prepupating larvae are reduced by the brevity of those two stages and their behavior in seeking hidden sites. Pupae are not readily accepted by the cannibalistic larvae because of their protective integument. Although younger larvae are subject to attack by older larvae, the latter develop speedily as a result of cannibalistic feeding and hence undergo ecdyses early, when they fall easy prey to the hungry younger larvae. This behavior may result in a more or less homogeneous population of larvae so far as age is concerned, when the host population is low. Cannibalism thus plays a significant role in preserving the species under conditions of shortage of food.

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БИБЛИОТЕКА

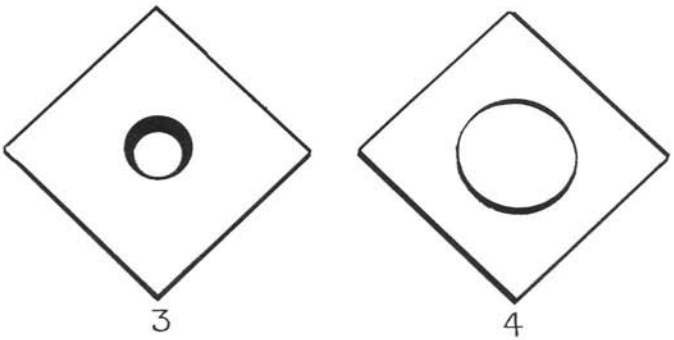
PLATE

PLATE 21

a. Cages, numbers 3 and 4, about actual size.

b. An assembled cage: 1, The cover; 2, The cage; 3, The balsa wood; 4, The petiole of the clover leaf; 5, A rubber band; 6, The clover leaflet.

c. Cages of various sizes, assembled and mounted on the stand.



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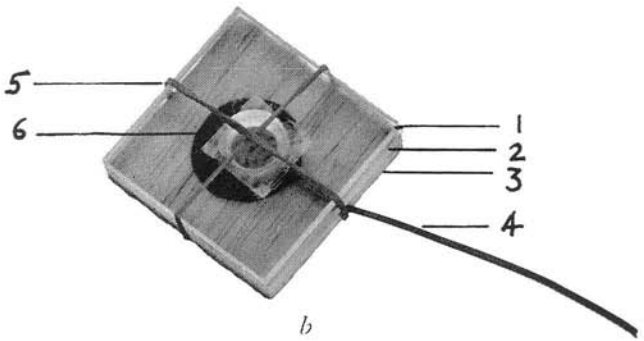

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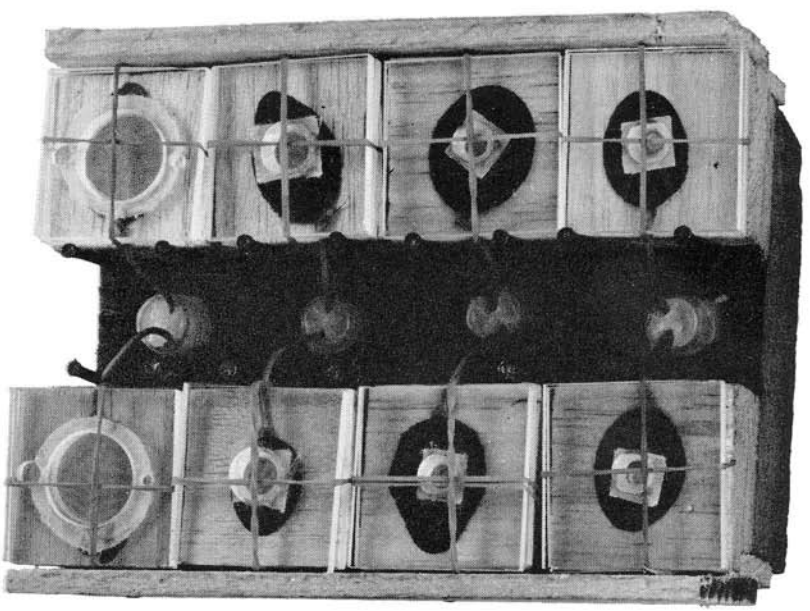

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