

smooth and shiny. Abdomen shorter than thorax, about as broad at base as long. Ovipositor not exerted.

Forewings pale at base, strongly embrowned in stigmal area, fading somewhat towards the apex. Post-marginal vein almost as long as stigmal vein; marginal vein short, barely longer than wide.

Male: unknown.

Type locality: I.C.T.A., Trinidad, B.W.I.

Type: U.S.N.M. No. 63502.

Remarks: Described from numerous specimens including holotype and paratypes reared from *Puto barberi* on cocoa in 1952 and 1953. Additional specimens have been obtained from the same host collected on several other plants including *Lantana camara* L., *Acalypha wilkesiana* Muell., *Gliricidia sepium* (Jacq.) and *Coccolobis wifera* L.

Zarhopalus is the only primary parasite that has been reared from *Puto barberi* in Trinidad. A few specimens of *Achrysothrips dactylopii* (How.), which emerged from *Puto barberi* were undoubtedly hyperparasitic on *Zarhopalus*.

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Laboratory Studies on the Food of Some Coccinellids (Coleoptera) Found in Ontario Peach Orchards¹

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Food habits and occurrence of the commoner species of coccinellids in peach orchards of the Niagara Peninsula, Ontario, are being investigated in connection with a study of the effects of pesticides on biological control agencies. Results of a study of *Stethorus punctillum* Weise have already been published (Putman, 1955). The present account deals with laboratory tests of feeding, mostly during June and July from 1952 to 1955, with prey of special economic importance in peach orchards.

The species concerned are *Coleomegilla maculata lengi* Timb., *Hippodamia convergens* Guer., *H. tredecimpunctata tibialis* (Say), *H. parenthesis* (Say), *Adalia bipunctata* (L.), *Coccinella transversoguttata* Fald. (vars. *quinquenotata* Kby., *nugatoria* Muls., and intermediate forms), *C. trifasciata perplexa* Muls., *C. novemnotata* Hbst., *Cycloneda sanguinea* (L.), and *Anatis quindecimpunctata* (Oliv.). Subspecific names will not be used subsequently.

General Methods

Field-collected adults were caged over aphid-infested chrysanthemums in the greenhouse or held individually in vials and supplied daily with aphids to obtain eggs from which the larvae and some of the adults used in the experiments were reared similarly. As the time and labour required to rear enough adults for all experiments proved prohibitive, field-collected adults were used in certain experiments as noted later. It was impossible to obtain adequate numbers of all species for some experiments because the species varied greatly in seasonal and yearly abundance and because some types of experimental prey were available only for a few days in the year.

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During the experiments the insects were kept individually in cotton-stoppered glass vials, either $\frac{1}{2}$ by 3 or 1 by 6 inches, depending on the instar of the predator and the type of prey. The vials were held in covered glass vessels containing dishes of a saturated solution of sodium chloride, which maintained a relative humidity of approximately 76 per cent at 20°C. The vessels were kept on a shelf outside the laboratory but sheltered from the sun.

The aphids, unless otherwise specified, were *Rhopalosiphum rufomaculatum* (Wilson), reared on chrysanthemum in the greenhouse. During the heat of midsummer this species did not thrive and the supply was sometimes augmented by field collections of other species. The two-spotted spider mite, *Tetranychus telarius* (L.), was from a greenhouse culture reared on broad bean, *Vicia faba* L. The European red mite, *Metatetranychus ulmi* (Koch), was collected from peach and plum orchards where no persistent insecticides had been used. Eggs of the oriental fruit moth, *Grapholitha molesta* (Busck), were obtained by caging adults from a laboratory stock or from field-collected larvae in glass jars lined with waxed paper. Eggs of *Pulvinaria vitis* (L.) were obtained by collecting ovisacs from peach orchards.

In some experiments the frass of the beetles was examined by softening the pellets in a drop of dilute sodium hydroxide solution on a slide, dispersing them in a drop of Hoyer's medium and covering them with a cover glass. The number of prey eaten was determined under a microscope by counting the more heavily sclerotized and easily identified fragments, such as the tips of the rostrum and the tarsi of aphids.

Feeding on Aphids

All of the species concerned have long been known to feed upon aphids of many species, and a number of authors, notable Clausen (1916) and others listed by Balduf (1935) and Clausen (1940), have given data on the rate of prey consumption by certain species. During the present studies the adults of all the species oviposited for long periods and the larvae were reared with low mortality when they were fed aphids, but most of these were in mass cultures and precise records were not kept.

A small-scale test was carried out to determine the rate of aphid consumption by adults of two species to furnish a standard to which the consumption of other prey could be compared. Field-caught adults were confined in vials with an excess of aphids, which were replenished daily. Three to six days after they were put in the vials, the frass produced during a 24-hour period was examined for aphid remains. The number of aphids represented in the frass produced during this period was assumed to equal the number eaten during a similar length of time. The frass of 16 of *A. bipunctata* contained remains of 0 to 129 aphids each, with an average of 32.0; that of 17 of *C. transversoguttata*, a larger species, contained 0 to 79, with an average of 47.3. Two of *A. bipunctata* and one of *C. transversoguttata* had apparently not fed on aphids for at least 24 hours; the refusal of other normally acceptable prey by some individuals can therefore be expected.

Feeding on Oriental Fruit Moth

Reared or collected adults were confined for three days, or longer, with eggs of the oriental fruit moth that had been laid on waxed paper. About 10 eggs were usually put in a vial. Sixteen out of 19 of *C. maculata* fed readily on the eggs. Most of the beetles began eating them on their first contact and usually ate all available, up to 28, within 24 hours. All of 11 reared larvae in the last two (third and fourth) instars ate the eggs equally as freely.

Of 22 adults of *H. convergens*, one, after refusing the eggs the first day, accepted them readily for three days, eating up to 64 per day; another ate 4 within three days, and the others refused them. Of 12 larvae, 3 ate small numbers of eggs, up to 14, within three days.

None of 8 adults of *H. parenthesis* ate the eggs, but 2 of 9 larvae ate up to 4 within three days.

One of 9 adults of *H. tredecimpunctata* ate one egg within 3 days.

None of 5 adults of *C. sanguinea* accepted the eggs; one of 9 larvae ate 5 eggs within 3 days.

Four of 13 adults of *A. bipunctata* ate up to 6 eggs and 5 of 15 larvae ate up to 5 eggs within 3 days.

Of 5 adults of *C. transversoguttata*, 8 of *C. novemnotata*, and 7 of *C. trifasciata*, none accepted the eggs. One of 5 larvae of *C. transversogutta*, one of 4 of *C. novemnotata*, and 3 of 6 of *C. trifasciata* ate not more than 3 within 3 days.

All of the coccinellids accepted aphids offered at the end of the experiment, except a few larvae that were about to pupate.

As the experiment was set up each coccinellid was watched until it had made contact with the eggs. Except most individuals of *C. maculata* and one adult of *H. convergens*, they did not appear to recognize the eggs as prey. The egg of the oriental fruit moth is lenticular and closely appressed to the leaf, and does not offer any obstacle as the beetle walks over it. It is possible that in those cases where only some of the eggs were consumed they had first been detached or lacerated by the claws of the coccinellids, which were very active.

Some of the eggs hatched in vials containing some individuals of all the coccinellid species in the experiment. The young larvae were invariably eaten.

Feeding on the Two-Spotted Spider Mite

Larvae newly hatched from eggs laid in confinement were supplied with bean leaves heavily infested with the two-spotted spider mite. The initial number of larvae and the percentage that reached the adult stage for each species were as follows: *C. maculata*, 17 and 100; *H. convergens*, 23 and 61; *H. parenthesis*, 15 and 80; *H. tredecimpunctata*, 15 and 60; *A. bipunctata*, 16 and 31; *C. sanguinea*, 13 and 15; *C. transversoguttata*, 16 and 0; *C. novemnotata*, 16 and 0; *C. trifasciata*, 16 and 0; *A. quindecimpunctata*, 8 and 0.

Most larvae of the three species of *Coccinella* died in the first instar; a few that reached the early second instar may have fed previously on the eggs of their own species. The larvae of *A. quindecimpunctata* died in the first to third instars. In the other species in which less than 100 per cent of the larvae reached maturity, mortality occurred throughout the larval and pupal periods. For example, in a series of 10 larvae of *A. bipunctata*, 1 died in the first instar, 3 in the second, 3 in the third, and 2 in the fourth, only one reaching maturity. Some of the adults in these species were also somewhat dwarfed.

Series of three species, *C. maculata*, *H. convergens*, and *A. bipunctata*, which had different levels of survival in the foregoing tests, were reared on the mite in comparison with parallel series reared on aphids to determine the relative effects of these foods on the duration of the larval period. The results (Table I) showed that larvae of *H. convergens* and *A. bipunctata* required nearly twice the time for development when fed mites as when fed aphids. The prolongation extended through all instars; for example, the mean durations of successive instars of *H. convergens* when fed aphids were 3, 3, 2, and 4 days, and when fed mites, 5.1, 3.1, 3.5, and 10.2 days. The difference in mean duration of the larval period of *C. maculata* was slight, although it was highly significant by Student's *t* test.

TABLE I

Durations of Larval Periods of Coccinellids Fed on Aphids and on Two-Spotted Spider Mite

Species	Food	Original Number of larvae	Number matured	Larval period, days	
				Range	Mean
<i>Coleomegilla maculata</i>	Aphids	10	10	11-12	11.7
	Mites	9	9	12-14	12.9
<i>Hippodamia convergens</i>	Aphids	8	8	12	12
	Mites	8	4	20-23	21.8
<i>Adalia bipunctata</i>	Aphids	10	9	14-15	14.3
	Mites	10	1	26	26

This slight difference was possibly due to lack in quantity of food rather than quality, for the older larvae that were given mites spent much more time in searching for this small prey than did those given aphids.

To determine the longevity of adults when fed on the two-spotted spider mite, series of newly transformed adults maturing in June and July were supplied with the mite for a maximum of 50 days. The larvae had been reared on aphids, except some of *C. maculata* that had been reared on the mite. The results (Table II) show that *C. maculata* survived much better than the other species. Directly comparable series fed on aphids were not available, but other work had shown that most adults of all the species lived longer than 50 days and often till at least the end of the season when fed aphids. As there was no consistent difference in longevity between the sexes the latter are not differentiated in the table. The great variation in longevity among individuals of some species, particularly

TABLE II

Longevities of Adult Coccinellids Fed on the Two-Spotted Spider Mite

Species	Original Number	Number living at		
		10 days	20 days	50 days
<i>Coleomegilla maculata</i>	13	11	11	8
<i>Hippodamia convergens</i>	12	11	4	2
<i>H. tredecimpunctata</i>	4	4	2	1
<i>Adalia bipunctata</i>	6	2	2	0
<i>Cycloneda sanguinea</i>	10	2	0	0
<i>Coccinella transversoguttata</i>	6	3	0	0
<i>C. novemnotata</i>	3	2	0	0
<i>C. trifasciata</i>	6	4	1	0

H. convergens, may have been due to some being in diapause. Most of large numbers of field-caught adults of most of the species died within four to six days when confined without food, but some of those caught in July and August and presumably in diapause lived up to 12 days. Diapause adults of *Stethorus punctillum* are also known to require less food than reproducing ones (Putman, 1955).

Except *C. maculata*, the adults in this experiment, as well as in others, fed upon the mites in a desultory manner very different from the way they attacked aphids. Some individuals, particularly of *Coccinella* spp., were never seen to attack the mites. It was obvious both from the observed rate of feeding and from the amount of frass produced that individuals feeding on mites ate a considerably smaller bulk of food than those feeding on aphids, again with the exception of *C. maculata*.

The next experiment confirmed the relatively short life of adults of most of the species when feeding on the two-spotted spider mite. None of the females in the foregoing experiment produced eggs, which was not conclusive because they had not been fertilized. Another experiment was therefore set up to test the effect of the mite as prey on egg production. Females reared on aphids or emerging from field-collected pupae were confined with males and fed aphids until they began to oviposit, when they were placed separately with two-spotted spider mites. All of 6 of *C. maculata* continued to oviposit until they were discarded after 24 to 60 days. Among 5 of *H. convergens*, 11 of *A. bimaculata*, 14 of *C. transversoguttata*, and 7 of *C. trifasciata*, none oviposited for more than 6 days; most died within 5 to 10 days and all within 17 days. *H. tredecimpunctata* behaved differently; all of 9 females ceased oviposition within two days after being given mites, but 5 were still living after 20 days. They were then given aphids, whereupon they resumed oviposition within 4 to 7 days. The lengths of the oviposition periods of the various species when feeding on aphids were not determined, but in routine rearing numbers of all the species were still ovipositing after one to two months.

Those coccinellids that fed upon the mite consumed all stages together with the webbing.

Feeding on the European Red Mite

Infestations of the European red mite dense enough to bring the larvae of the coccinellids to maturity or to support the adults for an appreciable length of time could not be found on foliage free of toxic spray residues. Enough mites were available to feed 10 newly hatched larvae of each of three species for 6 days; within that time all of *C. maculata* reached the third instar, a rate of development comparable to that of larvae fed aphids or two-spotted spider mites. Five of *H. convergens* reached the second instar and the others were more or less moribund, and all of *A. bipunctata* died in the first or second instar.

Reared or field-caught adults of several species, unfed for 12 to 18 hours, were confined with peach leaves on which the numbers of the European red mite had been artificially increased by brushing onto them the mites from other leaves with a mite-brushing machine (Henderson and McBurnie, 1943). They were closely watched for four hours. Fifteen of 18 of *C. maculata*, 7 of 17 of *A. bipunctata*, 1 of 11 of *C. trifasciata*, and 1 of 14 of *H. tredecimpunctata* were observed eating the mites; only *C. maculata* ate them freely. Of 3 adults of *H. convergens*, 2 of *C. sanguinea*, 18 of *C. transversoguttata*, and 14 of *C. novemnotata*, none ate any mites. At the conclusion of the experiment those adults that had refused mites were offered rose aphids, *Macrosiphum rosae* (L.), which were invariably attacked within a few minutes.

TABLE III
Numbers of Crawlers of *Pulvinaria vitis* Eaten in 24 Hours by Adult Coccinellids

Species	Number of beetles	Number eating crawlers	Number crawlers eaten	
			Maximum	Average
<i>Coleomegilla maculata</i>	11	9	123	24
<i>Hippodamia parenthesis</i>	3	3	5	4
<i>Adalia bipunctata</i>	15	8	26	4
<i>Coccinella transversoguttata</i>	10	3	13	7
<i>C. trifasciata</i>	10	6	36	11
<i>C. novemnotata</i>	5	2	5	1

Feeding on *Pulvinaria vitis* (L.)

Twelve adults and 6 larvae of *C. maculata*, 12 adults and 10 larvae of *A. bipunctata*, 7 adults of *C. transversoguttata*, and 12 adults of *C. trifasciata*, all unfed for three to four hours, were confined with intact ovisacs of *P. vitis* for 12 to 14 hours. None of the ovisacs were disturbed.

In a subsequent test the ovisacs were pulled apart to expose the eggs. Adult coccinellids were confined with the eggs for 16 to 18 hours and then held separately for two days, when the accumulated frass was examined. Seven of 10 of *C. maculata* and 3 of 11 of *A. bipunctata* ate 2 to 15 eggs each. None of 5 of *C. transversoguttata* ate any. Those observed eating or investigating the eggs were greatly hindered by the cotton of the ovisacs and the powdery substance mixed with the eggs and spent much time in cleaning their mouth parts.

Ten third- and fourth-instar larvae of *C. maculata*, 8 of *H. convergens*, 12 of *A. bipunctata*, and 7 of *C. trifasciata* were confined with eggs of *P. vitis* that had been shaken free from the ovisacs. Although a number of larvae were seen feeding on the eggs in a desultory manner, all were dead within seven days except one of *A. bipunctata*, which was near pupation at the beginning of the experiment and eventually produced an undersized adult. Before the larvae died some of the eggs had hatched, so that both eggs and crawlers were available as prey.

Adult beetles starved for 24 hours after feeding on aphids were confined for 24 hours with ovisacs from which newly hatched crawlers were emerging in large numbers. They were then held without food for three days and the accumulated frass was examined. Although crawlers were eaten by at least some individuals of all the species (Table III), the rate of consumption in terms of bulk, when the very small size of the crawlers is considered, was very much less than that of aphids as previously given.

Five adults of *C. maculata*, 5 of *H. convergens*, 8 of *H. tredecimpunctata*, 4 of *A. bipunctata*, 7 of *C. transversoguttata*, and 6 of *C. sanguinea* were confined for 24 hours with pieces of peach leaf bearing 4 or more scales of *P. vitis* in August, when the scales had nearly or quite reached maximum size for the season. Single scales were eaten by one adult of *C. maculata* and one of *C. transverso-*

guttata. As long as the scales remained in their usual position, closely appressed to the leaf, the beetles walked over them without any reaction. At least one of the scales eaten was crawling about the vial.

Behaviour on Encountering Prey

Fleschner (1950) and other authors have described the behaviour of several predators in the presence of their prey, involving a thorough search of the immediate vicinity of the first encounter. Such behaviour was shown strongly toward aphids by all the coccinellid species in the present study. If a beetle was following a fairly straight course when it met an aphid, it devoured it and then progressed more hesitantly and frequently turned from side to side as it explored the substratum with antennae and palpi. Not only living aphids but also their exuviae or honey dew often evoked this reaction. Encounter with less attractive prey usually did not induce searching behaviour; if an individual of most of the coccinellid species met a mite or a scale crawler it might devour that particular prey but seldom or never followed with such behaviour. In keeping with its wider range of prey, *C. maculata* showed typical searching behaviour not only with aphids but also with the two-spotted spider mite, the European red mite, and eggs of the oriental fruit moth.

Discussion

Although the interpretation of laboratory experiments on the selection of prey by predators is always doubtful, certain generalizations are evident. If a predator consistently refuses a particular species of prey in the laboratory or cannot develop normally on it, it can be safely concluded that it will be of no value in the natural control of that species in the field. If most individuals of a species eat only small numbers of the prey or if only occasional individuals eat it, the predator is also unlikely to be of importance. On the other hand, if a predator accepts the prey freely and especially if it develops normally when feeding exclusively upon it, the species is potentially important. Only species in this category are likely to exhibit the density-dependence characteristic of the most effective predators. Laboratory study thus serves to eliminate the unimportant species, so that only those likely to be influential need be given the field study needed to determine their true value.

By these criteria *C. maculata* is a potentially valuable predator with a wide range of prey; it fed freely on the two-spotted spider mite, the European red mite, and eggs of the oriental fruit moth, and it also attacked crawlers of *Pulvinaria vitis* more readily than the other coccinellids. Although the larvae developed normally on the two-spotted spider mite, natural infestations of this mite are very seldom dense enough to supply the large volume of food required by the older larvae, and the European red mite probably never reaches such a density. All the other species, as far as they were investigated, were primarily aphidophagous and had a much narrower range of acceptable prey; they fed only to a limited extent or not at all on the prey mentioned. *Coccinella* spp. had the most restricted range as the larvae of all three species did not develop on the two-spotted spider mite. None of the species tested ate the eggs or older nymphs of *Pulvinaria vitis* in any numbers. All fed readily on newly hatched larvae of the oriental fruit moth but on the trees these larvae are exposed for only a short time.

Because of its scarcity, little was learned about the food preferences of *A. quindecimpunctata*; also, *C. sanguinea* and some species of *Hippodamia* and *Coccinella* could not be included in all experiments. As the food habits of all species within each genus were very similar as far as they were investigated,

results for the species of *Coccinella* and *Hippodamia* more intensively studied may probably be true of the other local species of the same genera.

The range of prey of the larvae was in general similar to that of adults of the same species.

Some extension of the results to other prey not included in the investigations may be justified. The eggs of many Lepidoptera such as the codling moth, *Carpocapsa pomonella* (L.), and other olethreutids that are very similar to those of the oriental fruit moth should be assumed to be free from predation by most coccinellids until they are proved otherwise.

The avidity with which the prey was attacked, and whether it evoked searching behaviour, proved to be a good guide to its suitability, if allowance was made for the refusal of occasional individuals of the predator to attack any prey even after several hours without food. Although some species of prey not immediately attacked were eaten after several hours of confinement with the beetles, the numbers destroyed in such cases were always relatively small. It is true that many predators, including coccinellids, must spend part of their lives under semistarvation and therefore may accept relatively unattractive prey in the field, but coccinellids fly readily and are likely to leave environments where their preferred prey is scarce.

Summary

Coleomegilla maculata lengi Timb. fed readily on the two-spotted spider mite and the larvae developed normally on the same prey; this species also readily attacked the European red mite and eggs of the oriental fruit moth, and to a less extent the crawlers of *Pulvinaria vitis* (L.). *Hippodamia convergens* Guer., *H. tredecimpunctata tibialis* (Say), *Adalia bipunctata* (L.), *Coccinella transversoguttata* Fald., *C. trifasciata perplexa* Muls., and *Cycloneda sanguinea* (L.), in so far as they were tested, either refused the same species of prey or ate only small numbers after being deprived of food. Larvae of these species and of *Anatis quindecimpunctata* (Oliv.) could not develop normally on the two-spotted spider mite. Food preferences of the larvae were generally similar to those of adults of the same species. All the species mentioned are primarily aphidophagous except *C. maculata*, which is more or less polyphagous.

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