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broad geographic areas and various environmental conditions can be secured. It appears doubtful whether pea aphid colonies could survive long on clone no. 3, under field conditions in Kansas or Quebec exposed to predators, parasites and pathogens as well as weather conditions which are often adverse for the aphid.

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# Growth and Development of Coccinellid Larvae on Dry Foods (Coleoptera: Coccinellidae)

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## Abstract

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Ten species of predatory coccinellids representing seven genera were reared from the first-instar larva to the adult stage on dry powdered aphids. Dry pea aphids, Acyrthosiphon pisum (Harr.), and corn aphids, Rhopalosiphum maidis (Fitch), were both superior to bean aphids, Aphis fabae Scop., for growing coccinellid larvae. Though Anatis mali Auct. grew equally well on A. pisum and R. maidis, the larvae generally lived longer when starved after feeding on R. maidis. Dry aphids were as good as living aphids for growing A. mali and Coleomegilla maculata lengi Timberlake. C. maculata grew as well in darkness as in light, and an aphid-pollen mixture was superior to either component alone. Three generations of C. maculata were reared on a yeast diet and this diet is the most promising food for use to supplement natural foods in the field. An arrangement of coccinellid species on the basis of their food specificity does not correspond to the current phylogenetic arrangement, as the taxonomically primitive tribe Coccinellini contains both generalized and selective feeders.

#### Introduction

To investigate predator-prey relationships it is desirable to minimize or equalize both the searching activities of the predators and the escape responses of the prey. Certainly to make valid comparisons of the response of predators feeding on different prey it is necessary to control all non-nutritional factors that affect growth and development. These difficulties can be largely overcome by using dry powdered food. The predatory coccinellid *Coleomegilla maculata lengi* Timberlake was reared on dry powdered nymphs and adults of the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), and on various pollens (Smith 1960). Predatory species of coccinellids will eat various pollens in the laboratory, and in the field these and other species were found on pollenating plants that harbored few insect prey (Smith 1961). Pollen is probably the most important of the non-animal foods eaten by these predators.

This paper records the effects of various food materials on several coccinellid species and the development of a synthetic diet using *C. maculata* as the experimental animal.

#### Experiments

# General Materials and Methods

All the species of aphids used, except Acyrthosiphon pisum (Harr.) which was collected from alfalfa with a sweep net, were collected in the field by cutting the host plant and dropping it into paper bags. Within an hour after collection the nymphs and adult aphids were killed by freezing at  $-15^{\circ}$  C. Aphids were separated from larger insects and debris by means of sieves, then crushed with a mortar and pestle. The crushed aphids were desiccated in a freeze drier and then ground to a powder of particles not larger than corn pollen, i.e. 90 microns. Later freeze drying was discontinued when it was found that drying at room temperature over calcium sulphate did not affect the growth-promoting properties of the aphids. However, coccinellids fed on A. pisum that were dried at 100° C. for one half hour failed to grow whereas they grew normally when this aphid was dried at 20° C. for long periods. The dried aphids were stored at about  $-15^{\circ}$  C.

The adult coccinellids that were used to provide larvae for the experiments were fed on *A. pisum* or on diets containing Difco desiccated beef or liver. Firstand second-instar larvae of small species were reared individually in glass cells, 6 mm. deep and 1.9 cm. in diameter, and the later stages and all stages of large species were reared in petri dishes (Smith 1960). Sufficient food was placed on the floor of the cage so that the larvae always had an excess. A drop of drinking water was placed twice daily on the side wall of the cell for small larvae. Large larvae in petri dishes had a continuous supply of water in a dish. All experiments were done at  $21.9 \pm 0.7^{\circ}$  C. and about 65% R.H. A constant artificial light was used though natural light was admitted through the room windows.

The development and duration of each stage of the coccinellid larvae were recorded twice daily. The results were analysed by means of the F test and differences considered significant at the 1% level. Means and standard errors are given herein. Other materials and methods are described in context where applicable in the following seven experiments.

## (i) To Determine the Feeding Responses to Dry Aphids

Powdered A. pisum, R. maidis, and Aphis fabae Scop. were each tested as food for the larvae of 10 species of coccinellids: Adalia bipunctata (L.), Anatis mali Auct., Coccinella novemnotata Hbst., Coccinella transversogottata richardsoni Brown, Coccinella trifasciata perplexa Muls., Coleomegilla maculata, Cycloneda munda (Say), Hippodamia tredecimpunctata (Say), and Mulsantina sp. Sixteen to 79 first-instar larvae of each species were tested.

Eight of the ten species of coccinellids tested completed development to the adults stage on A. pisum, four on R. maidis, and one on A. fabae (Table I). C. novemnotata and C. trifasciata did not develop beyond the third instar while feeding on A. pisum. Unsatisfactory food usually greatly prolonged the last instar attained. With the exception of A. mali all species of coccinellids that completed development did so more rapidly on A. pisum than on R. maidis, though normal adults were produced on both foods. Only H. tredecimpunctata reached the adult stage on A. fabae, but these adults were smaller and the developmental time was significantly longer than on A. pisum and R. maidis. In addition seven first-instar larvae of A. mali were fed and completed their development on each of the following species of aphids: Dactynotus ambrosiae (Thomas), Eriosoma ulmi L., Hoplochaitphorus quercicola Monell, Macrosiphum rosae (L.), Myzus cerasi (F.), and Procphilus sp.

In some tests many coccinellids did not reach the second instar. Death may have resulted from non-acceptance of the food or from nutritional inadequacy. The latter is possible, as the results of the next experiment indicate.

## (ii) To Show the Deleterious Effect of A. fabae on C. maculata

Eighteen first-instar larvae of C. maculata were reared to the second ecdysis on dry A. pisum and then divided randomly into two equal-size groups; one was allowed to continue feeding on A. pisum, the other was put on A. fabae exclusively.

C. maculata reached the third instar on A. pisum in  $8.8 \pm 0.2$  days. The larvae that were transferred to A. fabae died four days later, whereas those remaining on A. pisum became adults in  $19.4 \pm 0.4$  days. This strongly suggests that A. fabae is nutritionally inadequate for C. maculata.

# (iii) To Compare the Effect of Previous Food on A. mali with and without Drinking Water

Unfed larvae of A. mali from the same egg masses were divided early in the first instar into two groups: one group of 15 larvae was given drinking water and the other group of 21 larvae was not. Other larvae from the same egg masses were divided similarly into two groups of at least 18 larvae each. One group was reared to the first ecdysis on R. maidis, and the other group was reared on A. pisum. Each group of these second instars was then subdivided equally and starved, but one lot received drinking water whereas the other did not. Additional groups were reared similarly to the second and third ecdysis on R. maidis and on A. pisum, and were subsequently starved and half of them given drinking water.

There was no significant difference between the longevities of unfed firstinstar larvae with drinking water  $(2.8 \pm 0.3 \text{ days})$  and those without  $(2.5 \pm 0.2 \text{ days})$ . But with the other instars drinking water increased the longevity of starving *A. mali* that had previously fed on *R. maidis* but not of those that had fed on *A. pisum* (Table II).

# (iv) To Compare the Effects of Dried and Living Aphids on the Growth of Coccinellids

Larvae from the same egg masses of A. mali and of C. maculata were divided into two groups of at least 15 individuals. One group of each species was fed on dry A. pisum and the other on living aphids that were reared on broad bean, Vicia faba L. The coccinellid larvae were weighed each day until pupation, and

Species	No.	First instar	Second instar	Third instar	Fourth instar	Pre-pupa	Pupa
			A. pisum			16	
Adalia bipunctata	22	$4.9 \pm 0.1$	$2.5 \pm 0.1$	$3.0 \pm 0.2$	$3.8 \pm 0.1$	$1.8 \pm 0.1$	$5_{-}0\pm0.2$
Anatis mali	37	$3.4 \pm 0.1$	$2.8 \pm 0.1$	$2.7 \pm 0.1$	$4.4 \pm 0.1$	$1.9 \pm 0.3$	$5.2 \pm 0.2$
Coccinella transversoguttata	34	$5.0 \pm 0.1$	$4.0 \pm 0.4$	$3.5 \pm 0.2$	$8.7 \pm 0.1$	$1.0 \pm 0.1$	$6.4 \pm 0.2$
Coleomegilla maculala	40	$3.7 \pm 0.2$	$2.8 \pm 0.2$	$2.9 \pm 0.3$	$4.3 \pm 0.4$	$1.0 \pm 0.1$	$3.5 \pm 0.3$
Cycloneda munda	30	$2.6 \pm 0.2$	$2.6 \pm 0.2$	$2.9 \pm 0.1$	$3.3 \pm 0.3$	$1.1 \pm 0.1$	$3.6 \pm 0.1$
Hippodamia parenthesis	16	$3.0 \pm 0.2$	$3.9 \pm 0.1$	$2.4 \pm 0.1$	$4.7 \pm 0.1$	$1.0 \pm 0.1$	$4.8 \pm 0.1$
Tippodamia tredecimpunctata	40	$3.9 \pm 0.2$	$2.9 \pm 0.2$	$3.3 \pm 0.3$	$4.6 \pm 0.6$	$1.0 \pm 0.1$	$4.7 \pm 0.3$
Mulsantina species	32	$3.9 \pm 0.1$	$3.3 \pm 0.1$	$4.0 \pm 0.9$	$3.9 \pm 0.2$	$1.0 \pm 0.1$	$5.4 \pm 0.3$
-1			R. maidis				
Adalia bipunctata	17	$5.4 \pm 0.1$	$2.7 \pm 0.1$	$2.9 \pm 0.2$	$7.5 \pm 0.5$	$1.0 \pm 0.1$	$5.4 \pm 0.1$
Anatis mali	27	$3.2 \pm 0.1$	$2.7 \pm 0.1$	$2.8 \pm 0.2$	$4.4 \pm 0.3$	$1.9 \pm 0.1$	$5.3 \pm 0.2$
Coleomegilla maculata	79	$3.8 \pm 0.1$	$3.3 \pm 0.1$	$4.1 \pm 0.2$	$5.4 \pm 0.3$	$1.0 \pm 0.1$	$4.4 \pm 0.2$
Hippodamia tredecimpunctata	32	$4.1 \pm 0.1$	$3.9 \pm 0.1$	$5.3 \pm 0.2$	$5.8 \pm 0.2$	$1.2 \pm 0.1$	$6_{+}2 \pm 0.1$
an a <b>p</b> arta manana any kaominina dia kaominina dia kaominina dia kaominina.			A. fabae				
Anatis mali	12	$4.9 \pm 0.1$	$7.8 \pm 0$	13.2			
Hippodamia tredecimpunctata	16	$7.1 \pm 0.3$	$6.1 \pm 0.2$	$6.1 \pm 0.1$	$8.9 \pm 0.2$	$1.4 \pm 0.1$	$5.6 \pm 0.1$

TABLE I
Mean and standard error of developmental time in days for various species and stages of coccinellids reared on dry A. pisum, R. maidis and A. fabae

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Treatment	Second	instar	Third instar		Fourth instar	
	Days lived	Difference between foods	Days lived	Difference between foods	Days lived	Difference between foods
Water No water	3.6(2.5) 3.1(2.1)	$1.1^{*}$ 1.0*	4.7(3.7) 3.5(3.6)	1_0* 0.1	$9_{6(5.5)} 6_{2(5.1)}$	4.1* 1.1
Difference between treatments	0.5(0.4)		1.2*(0.1)		3.4*(0.4)	

TABLE II

Mean longevity and difference between the means for unfed larvae of A. mali with and without drinking water and reared on R. maidis and A. pisum (in parenthesis)

\*Significant at 1% level.

the total time of development from first-instar larva to adult, the number that reached the adult stage, and the living weight of the adults were also recorded.

Results showed that *A. mali* required more time than *C. maculata* for development to the adult stage on both dry and living *A. pisum*, but there was no significant difference between the developmental times on the two foods within each species of coccinellid. With *A. mali* the duration was  $20.0 \pm 0.6$  days on dry food and  $20.0 \pm 0.7$  days on living food; with *C. maculata* 16.4  $\pm$  0.3 and 17.5  $\pm$  0.5 days, respectively.

The growth curves (Fig. 1) for *A. mali* show that living aphids were superior to dry aphids as food, especially during the last seven days, but, dry aphids were consistently better for growth of *C. maculata*.

Fourteen or 70% of the 20 *A. mali* that were reared on dry *A. pisum* became adults and averaged  $35.9 \pm 2.6$  mg. in weight. Nine or 60% of the 15 *A. mali* reared on living *A. pisum* became adults and averaged  $38.8 \pm 1.7$  mg. For *C. maculata* on dry *A. pisum* results were 90% survival and adult weight of  $12.0 \pm 1.0$  mg.; for 20 on living aphids, 30% and  $8.5 \pm 0.3$  mg., respectively.

# (v) To Determine the Effects of Light on C. maculata

From the same egg masses 20 first-instar larvae of C. maculata were divided into two equal groups, one of which was reared in continuous artificial light and the other group in darkness. The dark-reared group was exposed to weak artificial light for two minutes each day during servicing. Both groups were fed dried A. pisum, which was provided as needed in 5.0-mg. lots. The total food intake was determined by subtracting the food left, after removal of excrement, from the sum of the food lots given. The criteria used in this experiment to determine the effect of light were developmental time, dry weight of adult, and indices of relative food intake, of relative growth, and of food efficiency.

To calculate the indices of relative food intake, of relative growth, and of food efficiency, it was necessary to record: the initial body weight of *C. maculata*, W1; the final body weight, W2; the total food intake, F; and the time interval, i.e. the duration of the test, T. The weights of the adult predators and the food aphid were measured in milligrams dry weight, and the time in days. However, the initial dry weight of the unfed first instar of *C. maculata* was calculated on the basis that it contained 74% of water. From these data were calculated the average weight of each individual,  $W = \frac{1}{2} (W1 + W2)$ ; the weight increase,

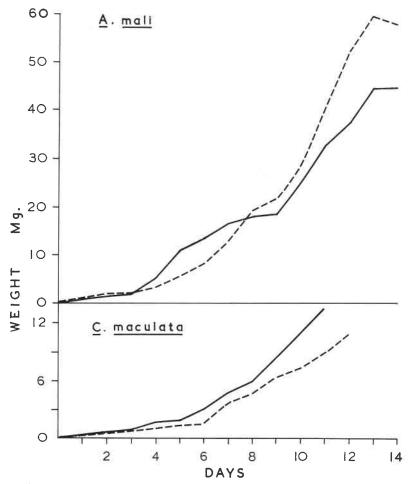


Fig. 1. Upper graph: effects of dry A. pisum (solid line) and living A. pisum (broken line) on the growth of A. mali. Lower graph: the same relationships for C. maculata.

w = W2 - W1; and the index of relative food intake, F/T  $\times$  W: the index of growth, w/T  $\times$  W; and the index of food efficiency, w/F.

As no significant differences were found between the means of the criteria with regard to light exposure, the data may be combined. The developmental time of *C. maculata* was  $18.2 \pm 0.7$  days, the adult weight was  $2.2 \pm 0.1$  mg., the relative food intake was  $0.40 \pm 0.01$  mg. per day, the growth was  $0.10 \pm 0.00$  mg. per day, and the food efficiency was  $0.20 \pm 0.01$  mg.

# (vi) To Compare the Effects of an Aphid–Pollen Mixture with Each Component Alone

First-instar larvae from the same egg masses of C. maculata were divided into three groups. The first group of 24 larvae was fed on dry R. maidis, the second of 40 on corn pollen, Zea mays L., and the third of 20 on a mixture of R. maidis and corn pollen (1:1 by weight).

It was found that the developmental time to adults of *C. maculata* on *R. maidis* was  $23.9 \pm 0.1$  days; on corn pollen,  $26.0 \pm 0.3$  days; and on the mixture,  $22.1 \pm 0.1$  days. The survival on *R. maidis* was 25%; on corn pollen, 15%; and on the mixture, 65%.

Food		Developm	Survival %		
F1	F2	F1	F2	F1	F2
Hemp pollen	Yeast	$23.7 \pm 1.4$	$32.4 \pm 1.0$	45	50
Hemp pollen	Liver	$23.7 \pm 1.4$	39 +	45	<1
Hemp pollen	Birch pollen	$23.7 \pm 1.4$	$23.1 \pm 1.0$	45	66
Yeast	R. maidis	$21.3 \pm 0.3$	$27.9 \pm 1.6$	86	75
Yeast	Yeast	$21.3 \pm 0.3$	$33.5 \pm 1.7$	86	49
	Yeast	$22.9 \pm 1.9$	$36.4 \pm 2.0$	52	50
Corn pollen Corn pollen	Corn pollen	$22.9 \pm 1.9$ $22.9 \pm 1.9$	$26.0\pm1.3$	52	50

 TABLE III

 Mean and standard error of developmental time and approximate percentage survival for first and second generation larvae of C. maculata fed various dry foods

# (vii) To Compare the Effects of Synthetic Diets, Pollens, and R. maidis

Larvae of C. maculata were fed several synthetic diets. The best diet for growth contained 40% by weight brewer's yeast powder (Mead Johnson of Canada, Belleville, Ontario). The other ingredients and their approximate percentage compositions were: sucrose, 55; cholesterol, 0.3; salt mixture (McCollum and Davis), 1.5; ribose nucleic acid, 1.5; wheat germ oil, 1.5; choline chloride, < 0.1; inositol chloride, < 0.1; and B vitamins.<sup>1</sup> Adults were fed a diet that contained 40% Difco liver and with the other ingredients the same as in the yeast diet. These diets were prepared by dehydrating an aqueous mixture of the ingredients and grinding the residue to a fine powder.

First-instar larvae from the same egg masses of *C. maculata* were divided into three equal groups each of 50 larvae. The first group was fed on the pollen of hemp, *Cannabis sativa* L., the second on the yeast diet, and the third on corn pollen. Second generation larvae from the same egg masses, the progeny of individuals reared on hemp pollen, were divided into three groups each with 20 larvae. The first group was fed the yeast diet, the second group was fed the liver diet, and the third group was fed the pollen of birch, *Betula populifolia* Marsh. Progeny of individuals reared on the yeast diet were divided into two groups each with 20 larvae. One group was fed *R. maidis*, and the other the yeast diet. Similarly progeny of individuals reared on corn pollen were divided into two groups of 20 each. One of these was reared on the yeast diet and the other on corn pollen. The total time of development and number that reached the adult stage were recorded for all groups (Table III).

In another test three generations of C. maculata larvae that were fed the yeast diet were compared to three generations that were fed R. maidis. Total developmental time and survival were the criteria used. At least 60 larvae were started on each food in the first generation, 35 in the second, and 16 in the third.

The time of development in days for each of three generations of *C. maculata* reared on the yeast diet and dry *R. maidis* (in parenthesis) was: first generation— $21.3 \pm 0.3 (23.3 \pm 1.0)$ ; second generation  $- 33.5 \pm 1.7 (27.9 \pm 2.5)$ ; and third generation  $- 33.7 \pm 1.2 (26.7 \pm 5.7)$ . The approximate percentage survival for three generations of *C. maculata* reared on the yeast diet and dry *R. maidis* (in parenthesis) was: first generation - 86 (66); second generation - 49 (75); and third generation - 36 (44).

<sup>&</sup>lt;sup>1</sup>Approximately 5.0 mg. niacinamide, 2.5 mg. calcium pantothenate, 1.5 mg. thiamin hydrochloride, 1.2 mg. riboflavin, 1.2 mg. pyridoxine hydrochloride, 0.1 mg. folic acid, 0.02 mg. biotin and 0.002 mg, vitamin B12 were added for each 10 g. of diet.

# Discussion

Dry powdered food may be used to further our knowledge of predator-prey relationship and perhaps increase the numbers of a predator when used in the field. It allows a number of experiments to be done with the same batch of identical food material, and it permits control over the water consumption of the predator as the succulence of living prey is no longer a factor. Powdered food can be manipulated more easily than living prey, and may be used to determine the indices of relative food intake, relative growth, and food efficiency. These indices may be used as criteria for comparing the responses of various species to changes in food quality and quantity.

The percentages of the total developmental time spent in the first and second instars, in the third and fourth instars, and in the pupal stage for the species that were reared on *A. pisum* and *R. maidis*, with the pre-pupa included with the last larval stage for comparison with Balduf's (1935) data (in parenthesis), are: first and second instars, 32% (32%); third and fourth instars, 45% (42%); and pupa, 23% (26%). Balduf's species were reared on different species of living aphids and under variable conditions of temperature. However, food quality unless very low, i.e. *A. fabae* for most species in this study, does not affect the relative duration of stages much, and Kaddou's (1960) data for *Hippo-damia quinquesignata* (Kirby) and Hodek's (1958) for *Coccinella septempunctata* L. show that temperature does not much affect the relative duration of stages. In the present work the duration of the first-instar larva usually exceeded that of the second instar by about 36%. This is in agreement with Balduf's conclusion that the second instar is shorter than the first.

As all species accepted dry, powdered food, visual stimuli, such as prey movement, shape, size, color, and texture, are of little importance for the perception of food. This is supported by *C. maculata's* ability to develop normally in darkness. Banks (1957), Dixon (1958), and Fleschner (1950), working with different species, reported that coccinellid larvae perceive their prey only by physical contact. This may be the reason why many species are unable to survive at low prey densities. To increase survival in the field under these circumstances it would be necessary to use large quantities of a powdered food supplement, and distribute it widely over the area searched by larvae.

The species that were successfully reared on dry foods did not belong to one taxonomic group or even to closely related groups. The most primitive and widely distributed tribe contained species that were reared, i.e. *A. mali* and *A. bipunctata*, and those that could not be reared, i.e. *Coccinella* spp. The species of *Hippodamia* and *Coleomegilla* responded as well as *A. mali*, though they belong to taxonomically more advanced tribes, the Hippodamini and Anisostictini respectively. Of the primitive species studies *A. mali* is the most generalized feeder and of the more advanced species *C. maculata* and *H. tredecimpunctata* are the most generalized feeders and would probably respond to dry supplemental foods in the field.

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# Morphologie Larvaire des Agrilus liragus Barter et Brown et Agrilus anxius Gory (Coleoptera: Buprestidae)<sup>1</sup>

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#### Abstract

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A detailed description of the larva of Agrilus liragus Barter and Brown, and the distinctive characters of Agrilus anxius Gory are given with a short discussion on the taxonomic value of some morphological characters.

### Introduction

Au cours d'une étude d'ensemble sur les Buprestides du Québec, j'ai eu l'occasion de récolter un certain nombre de larves d'Agrile sous l'écorce du peuplier tremble (*Populus tremuloides* Michx.) et du bouleau à papier (*Betula papyrifera* Marsh.). Ces larves élevées jusqu'au stade adulte permirent de vérifier qu'il s'agissait, pour celles rencontrées sur la première essence, de l'Agrilus liragus Barter et Brown et pour celles sur la seconde essence de l'A. anxius Gory. On sait, depuis le travail de Barter et Brown (1949) qu'il est très difficile de séparer ces deux espèces à l'état adulte et encore plus à l'état larvaire. Il nous a paru intéressant de rechercher chez les larves des caractères qui permettraient de les identifier en toute sûreté. Dans le présent travail la larve de l'A. liragus est décrite en détail et les caractères morphologiques propres à l'A. anxius sont simplement énumérés.

### Matériel et techniques

Les deux groupes de peupliers trembles échantillonnés, d'un diamètre de 4 à 5 pouces et de 7 à 8 pouces respectivement, faisaient partie de deux peuplements purs contigus de la section forestière L.8 (Rowe 1959), à six milles au sud de Ville-Marie. Les bouleaux à papier d'un diamètre de 4 à 8 pouces provenaient d'un peuplement mélangé situé dans la section forestière L.4 (Rowe 1959), à cinq milles au nord de Laniel.

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