Effects of Food on the Longevity, Fecundity, and Development of Adult Coccinellids (Coleoptera: Coccinellidae)

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Abstract

Canad. Ent. 97: 910–919 (1965)

Access to drinking water increased the longevity of *Coccinella trifasciata perplexa* Muls. by about 35%. The water content of field-collected insects was 70% and of laboratory-fed insects 64%. Rate of loss of water increased, and longevity decreased when protein was absent from the food.

Anatis mali Auct. lived more than 1000 days and *Coleomegilla maculata lengi* Timberlake lived more than 400 days when fed on various synthetic foods. Seven of 13 species tested laid eggs when fed on these foods. A diet containing desiccated liver was the best non-prey food supplement for reproduction, and adults of three generations of *C. maculata* were kept on this food.

A. mali preferred dry powdered pea aphids, *Acyrthosiphon pisum* (Harr.), to either bean aphids, *Aphis fabae* Scop., or corn aphids, *Rhopalosiphum maidis* (Fitch), whereas *C. maculata* preferred corn pollen to aphids and *A. pisum* and *R. maidis* to *A. fabae*. Previous feeding did not affect the preference of either *A. mali* or *C. maculata* for dry aphids or pollen. *C. maculata* produced six eggs per mg. of food while feeding on *A. pisum* and four on *R. maidis*. Young adults ate more than older adults.

The rate of food intake was highest in *A. mali* during the first two weeks and in *C. maculata* during the first eight days after emergence. The living weight and dry weight of feeding *C. maculata* adults increased for eight days and then did not vary, whereas the water content decreased in this period. The index of relative growth was about 0.10 mg. per day per mg. of adult weight and food efficiency was about 0.18 mg. per mg. of food.

Introduction

The effectiveness of predatory coccinellids as mortality agents of aphids and other insect prey is limited by their inability to survive where prey are scarce. They are thus unable to prevent a rapid increase in numbers of prey that occurs in the early stages of an infestation. The numbers of a predator and its synchronization with the prey are regulated by many factors, most of which cannot be easily manipulated. Coccinellid females settle and lay their eggs on or near plants that contain their aphid food (Banks 1956; Dixon 1959); they also eat various non-prey foods (Putman 1964). Synthetic foods may be used to increase the survival of coccinellid adults and also perhaps to aggregate ovipositing females in places where aphids are expected to occur in large numbers. For this to be done, information on the effects of food quality and quantity on coccinellid adults is required.

The effects of drinking water, food quality, and synthetic foods on the longevity, reproduction, and survival of adult coccinellids are described in this paper. The effects of a predator's preference and age on the quantities of food eaten are also reported.

Materials and Methods

The origins of the adult coccinellids were described by Smith (1958). The species were: *Adalia bipunctata* (L.), *Adalia frigida* (Schn.), *Anatis mali* Auct., *Coccinella novemnotata* Hbst., *Coccinella transversoguttata richardsoni* Brown, *Coccinella trifasciata perplexa* Muls., *Coleomegilla maculata lengi* Timberlake, *Cycloneda munda* (Say), *Hippodamia convergens* (Guérin-Meneville), *Hippodamia glacialis glacialis* (F.), *Hippodamia parenthesis* (Say), *Hippodamia tredecimpunctata tibialis* (Say), and *Mulsantina* sp.

The adults were kept in petri dishes and dry food and water were provided separately (Smith 1960). Dry powdered aphids were used in place of living aphids (B. C. Smith, in preparation). The work was done at 21.9 ± 0.7° C. and about 65% R.H. A constant artificial light was used though natural light was admitted through windows. Results were analysed by means of the F test and differences considered significant at the 1% level. Means and standard errors or ranges are given. Other materials and methods are described where applicable.

Effects of Drinking Water and Food Quality on Longevity

Overwintered adults of *Coccinella trifasciata perplexa* Muls. were collected from alfalfa in June. They were sexed using the characters of the head described by Dobzhansky (1931) and divided into two similar groups, each with 32 females and 32 males. They were weighed individually and confined singly in petri dishes. Half the females and half the males of the first group were given distilled water to drink but no food, and half was given neither water nor food. They were inspected at least three times daily. The life span and dry weight of each was recorded.

Half the females and half the males of the second group were fed a dry food mixture that contained 40% dry weight Difco liver. The other ingredients and method of preparation are described elsewhere (Smith, in preparation). The other half was fed the same mixture, but with liver replaced by a non-nutritive bulk, alphacel (Nutritional Biochemicals Co.). These foods and water were provided in excess for 28 days. The insects were then confined without food and water and their subsequent loss in weight was determined each day. The life span of each was recorded, and after death, their dry weights were determined.

The percentage weight loss for all insects was calculated from the initial living weights and the final dry weights. In the second group the daily weight losses were calculated as a percentage of the initial weight, the weight loss at death was calculated from the final living weight, and the final dry weight, and the relationship between weight loss and length of life was determined.

Without water, the females of the first group lived 7.1 ± 0.6 days and the males 5.1 ± 0.3 days; the difference was significant. With water, females lived 9.2 ± 1.5 days and males 7.1 ± 0.5; the difference was significant. Although females were significantly heavier than males (17.2 ± 0.7 mg. and 4.8 ± 0.3 mg. respectively for the living and dry weights of females and 12.4 ± 0.4 mg. and 3.8 ± 0.5 mg. for males) the weight loss was about 70% for all insects kept with water and without water.

The insects of the second group ate both foods and produced solid excreta during feeding but none during starvation. No eggs were laid and the insects did not move except to feed. Both sexes lived significantly longer when starved after eating the liver or protein diet than after eating the non-protein diet. After eating the protein diet, females lived 16.3 ± 1.5 days and males lived 13.4 ± 1.4 days. After eating the non-protein diet, females lived 10.6 ± 1.4 days and males lived 6.6 ± 1.2 days.

The living weight of both sexes was significantly greater after eating the protein diet (21.7 ± 0.9 for females and 17.9 ± 0.5 for males) than after eating the non-protein diet (18.6 ± 1.0 for females and 15.5 ± 0.7 for males). Food quality had no effect on the final dry weights after starvation (7.0 ± 0.5 for females and 6.0 ± 0.6 for males) and on the total weight loss which was about 64% in both sexes. The weight loss at death was 36% for females after eating both diets and males after eating the protein diet. It was significantly lower at 26% for males after eating the non-protein diet. The greatest weight loss for

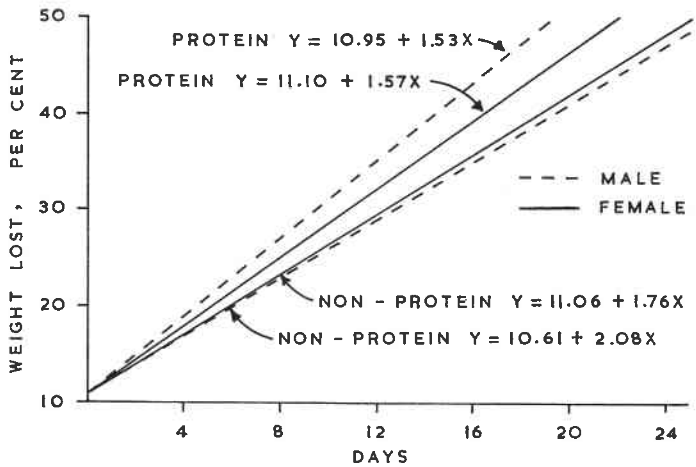

Fig. 1. Percentage weight lost by unfed males and females of *C. trifasciata* after feeding on protein and non-protein foods.

both sexes occurred on the first day of starvation. When both sexes were fed on the non-protein diet (Fig. 1), the relationship between the daily weight losses and longevity did not significantly deviate from linearity and the rate of loss of weight was significantly greater than when the insects were fed on the protein diet.

When adults were kept without food and water, increases in their weight were caused by the oxygen taken in and decreases were caused by losses in water, carbon dioxide, and excreta. Losses of weight in the form of carbon dioxide were small in comparison to those caused by water losses. Weight losses caused by the production of excreta were small after the first day. It may therefore be concluded that the weight lost by the insects in these experiments is a representative measure of the rate of water loss.

Effects of Various Synthetic Foods on Longevity and Reproduction

A number of moist and dry foods were fed to adults of the 13 species of coccinellids listed. *Coleomegilla maculata* was further tested on five additional dry diets.

The moist foods were fresh, minced pork liver and a diet based on fresh bananas (banana 90.0%, casein 9.0%, wheat germ oil 0.9% and B vitamins[1] about 0.1%). The dry foods were: alpha protein, casein, corn meal, and egg albumen (all from Nutritional Biochemicals Co.), desiccated Difco beef, and Difco liver, brewer's yeast (Mead Johnson of Canada, Belleville, Ontario), mixed baby cereal (Mead), and sucrose. The approximate compositions of three dry food mixtures were: (1) Difco egg-meat 40%, yeast 30%, and sucrose 30%; (2) casein 40%, yeast 10%, and sucrose 50%; (3) Difco liver 40%, yeast 10%, and sucrose 50%.

The effects of five dry diets on *C. maculata* were compared with the effects of feeding dry, powdered *R. maidis*. The protein sources comprised about 40% in four of the diets and were: desiccated beef, egg albumen with 5% isoleucine, desiccated liver, and yeast. The fifth diet contained alphacel in place of protein.

[1]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.

TABLE I

Foods accepted (A) and promoting egg production (E), and longevities for adults of various coccinellid species fed on various synthetic foods

Species	Food					Longevity
	Fresh liver	Banana diet	Dry mix 1	Dry mix 2	Dry mix 3	
A. bipunctata	A	E	A		E	66.4 (55–88)
A. frigida		A	A	E	A	121.4 (45–173)
A. mali	E	E	A	A	E	52.6 (26–87)
C. novemnotata		A				21.8 (17–36)
C. trifasciata	A	A	A	A	A	55.1 (43–72)
C. transversoguttata		A				66.8 (27–112)
C. munda	A	E				53.7 (33–126)
H. convergens	E	E	A	E		134.3 (76–167)
H. glacialis		E	A			120.6 (78–198)
H. parenthesis	A	A	A	A	A	40.8 (29–75)
H. tredecimpunctata	A	E	A	A	A	55.3 (36–108)
Mulsantina sp.		A		A	A	134.3 (106–191)

All diets contained approximately 55% sucrose, 0.3% cholesterol, 1.5% salt mixtures (McCollum and Davis), 1.5% ribose nucleic acid, 1.5% wheat germ oil, and less than 1% choline chloride, inositol chloride, and B vitamins.

At least 20 adults of each species were fed a test food individually in a petri dish. Feeding was confirmed by the production of excreta. A test was discontinued within 15 days if adults did not feed or if mortality was over 50%. When large quantities of excreta were produced, a test was continued for a month or longer. Eggs were attributed to a particular food only when laid by females that had fed a minimum of 10 days on the food. This period was selected because gravid females from the field invariably stopped oviposition within 10 days of being confined with food that was inadequate for egg production.

Some foods and diets, though not adequate for reproduction, served to maintain life for extended periods. *A. mali* lived over 1000 days and *C. maculata* over 400 days. A similar tendency was observed in other species. *C. maculata* ate all the foods and food mixtures offered, but laid eggs only when fed on fresh liver, the banana diet, and dry mixtures 1 and 3. Adults lost some of their red pigmentation when feeding on sucrose. The mean and range (in parenthesis) of *C. maculata's* longevity in days when fed on various dry foods were: alpha protein 15.6 (9–21), casein 29.7 (5–60), corn meal 42.7 (11–74), egg albumen 33.1 (17–43), beef 21.4 (15–27), liver 42.2 (26–59), yeast 47.9 (25–75), baby cereal 31.2 (18–54), and sucrose 26.4 (19–32). The other 12 species were more selective feeders than *C. maculata* but six of them laid eggs when kept on some of the foods (Table I).

Gravid field-collected females of *C. maculata* stopped laying eggs after three days of feeding on the diet that contained no protein. The number of eggs laid per female per day, the number of eggs per cluster, and the time interval in days between clusters for the other four diets were:

	Beef	Egg	Liver	Yeast
Eggs per day	4.6 ± 1.0	3.3 ± 0.5	4.3 ± 0.7	3.6 ± 0.3
Eggs per cluster	13.2 ± 0.7	10.5 ± 1.0	11.0 ± 0.9	10.0 ± 1.0
Interval, days	3.8 ± 0.8	4.6 ± 0.8	3.4 ± 0.5	3.6 ± 0.5

Both fecundity and fertility of the adults fed on the synthetic diets decreased with age, but there was no decline in the fecundity of females fed on *R. maidis*. The liver diet was superior to the others for reproduction in the laboratory-reared generations of *C. maculata*. Adults of the first laboratory generation fed on yeast diet laid no eggs, although this diet was superior to the others for growth of larvae. Two generations of liver-fed *C. maculata* adults that emerged from yeast-fed larvae were smaller and had lower reproductive capacities than field-collected adults:

	Field-collected	First generation	Second generation
Eggs per day	4.4±0.9	2.4±0.2	1.5±0.4
Eggs per cluster	11.2±2.9	8.7±0.4	6.9±0.2
Interval between clusters, days	4.2±0.6	5.6±2.1	8.3±2.1
Eggs hatching, per cent	50	17	11

Effects of Various Factors on Food Intake, Rate of Food Intake, and Reproduction

Preference

Adults of *A. mali* and *C. maculata* were given the choice of eating *A. pisum*, *A. fabae*, or *R. maidis*. The food was placed in separate containers in a petri dish that contained either five adults of *A. mali* or eight of *C. maculata*. Forty adults of each species were observed for 35 days, and the weight of the food ingested by each group was determined and recorded. Each food aphid was replaced as it was eaten. Food was measured with a specially designed spatula that held 7.1 mg. of *A. pisum*, 16.8 mg. of *A. fabae*, or 9.6 mg. of *R. maidis*. Adults of *A. mali* were obtained from larvae that were reared on *A. pisum* and those of *C. maculata* were collected from corn.

The effect of previous feeding on the food preference of *A. mali* was determined. Sixteen first-instar larvae of *A. mali* were reared to the adult stage on *A. pisum* and 16 were reared on *R. maidis*. Of the adults reared on *A. pisum*, eight were fed on this aphid for 14 days and then given the choice of measured quantities of *A. fabae* and *R. maidis*, and eight were fed on *A. pisum* for 94 days after emergence. Of the adults reared on *R. maidis*, eight were fed on this aphid for 14 days and then given a choice of measured quantities of *A. fabae* and *R. maidis* and eight were fed on *R. maidis* for 94 days after emergence. The coccinellids were reared singly in petri dishes.

The effect of previous feeding on *C. maculata* was also studied. Three groups each of 24 adults collected from corn were fed on each of *A. pisum*, *A. fabae*, and *R. maidis* for 21 days, after which they were given the choice of measured quantities of at least three foods for 30 days. The *A. pisum* and *A. fabae* groups were given *A. pisum*, *A. fabae*, and *R. maidis*, and the group reared on *R. maidis* was given the same three aphids and also corn pollen. Eight adults were confined in a dish and the measuring spatula held 16.8 mg. of corn pollen.

Adults of *A. mali* ate much more *A. pisum* than either *A. fabae* or *R. maidis*, whereas adults of *C. maculata* ate about equal quantities of *A. pisum* and *R. maidis* and much less of *A. fabae*. When given a choice for 35 days, five *A. mali* ate 49.0 (42.0–57.5) mg. of *A. pisum*, 8.7 (5.3–19.0) mg. of *A. fabae*, and 14.0 (7.0–28.5) mg. of *R. maidis*. In the same period eight *C. maculata* adults ate 50.4 (2.8–98.0) mg. of *A. pisum*, 16.8 (1.9–22.4) mg. of *A. fabae*, and 44.8 (2.5–67.2) mg. of *R. maidis*.

The quality of food previously eaten did not affect the preference of *A. mali*. Adults that were reared and fed on *A. pisum* each ate 16.1 (12.3–20.6) mg. of *A. fabae* and 22.4 (15.8–26.3) mg. of *R. maidis* in 80 days, whereas adults that were fed exclusively on *A. pisum* ate 39.2 (29.3–45.6) mg. of this aphid. Adults that were reared and fed on *R. maidis* each ate 12.2 (11.3–19.5) mg. of *A. fabae*, and 14.4 (9.6–18.4) mg. of *R. maidis* in 80 days and those fed exclusively on *R. maidis* ate 31.6 (20.4–41.0) mg. of this aphid.

Previous feeding did not affect the food preference of *C. maculata* and corn pollen was preferred to aphids as follows:

	Food and quantities eaten by 8 adults, mg.			
First food	*A. pisum*	*A. fabae*	*R. maidis*	Corn pollen
A. pisum	14.4 (10.0–17.1)	19.2 (15.6–24.3)	12.0 (8.6–17.2)	
A. fabae	16.8 (13.2–20.5)	14.8 (11.4–19.7)	20.1 (16.5–24.9)	
R. maidis	0	0	17.5	57.6 (51.3–64.8)

Preference and Age

The quantity of food eaten by young adults of *A. mali* was determined. Twenty adults that emerged from larvae that were reared on *A. pisum* were divided into two equal groups. The first group was individually fed on weighed quantities of *A. pisum* for 14 days and the second was given a choice of eating *A. pisum* or *R. maidis*. The same procedure was followed with 20 adults that emerged from larvae that were reared on *R. maidis*. The first group was fed *R. maidis* and the second was given a choice of *A. pisum* or *R. maidis*.

Adults of *A. mali* ate food at a greater rate within 14 days than within 30 or 80 days of emergence. Adults that were given a choice of foods ate more than those confined to one food. The quantity of food eaten by an adult within 12 days of emergence was:

	Adult food eaten, mg.	
Larval food	*A. pisum*	*R. maidis*
A. pisum	46.2±2.8	
R. maidis		51.8±5.6
R. maidis	42.0±7.0	15.4±7.0
A. pisum	61.6±15.0	32.2±4.2

Rate of Food Intake

The rate of food intake was determined periodically for adults of *A. mali* feeding on measured quantities of *A. pisum* and for males and females *C. maculata* feeding on measured quantities of each of *A. pisum*, *A. fabae*, and *R. maidis*. The tests were continued for about 50 days with 12 adults of *A. mali* and 12 of each sex of *C. maculata*. Four adults were confined to a dish. The *A. mali* adults were reared as larvae on *A. pisum* and were young and previously unfed. The *C. maculata* adults were collected from corn in the field. Each determination of rate was found by dividing the total quantity of food eaten in a dish by the time required for consumption and the number of insects. Food was measured in milligrams and time in days. The rates of the replicates were averaged. Deter-

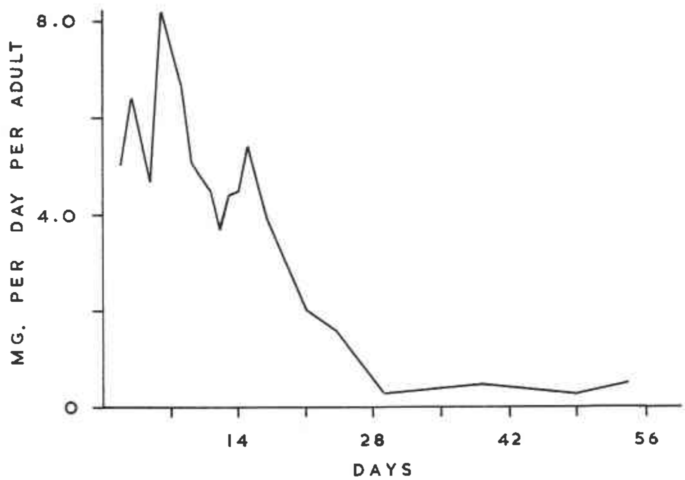

Fig. 2. Relationship between the rate of food intake of *A. mali* adults and age.

minations were made at least once every 10 days and more often when much food was eaten.

The rate of food intake of adults of *A. mali* was higher than 4 mg. per day per adult for the first two weeks of feeding; it then declined and remained at a much lower level (Fig. 2). The rate of food intake of *C. maculata* was consistently higher for females than for males and it varied much during the 50-day test period (Fig. 3).

Reproduction

The quantity of food eaten and number of eggs laid were determined for two females of *C. maculata* that were fed on each of *A. pisum*, *A. fabae*, and *R. maidis*. After copulation, the females were fed individually in petri dishes. Eggs were incubated at room temperature, and after five days classified as hatched, dead embryos, or no development. Eggs showing no development remained yellow, whereas those with dead embryos were dark in colour.

C. maculata produced about six eggs per milligram of food while feeding on *A. pisum* and about four eggs per milligram on *R. maidis*. Both aphids were much superior to *A. fabae*:

Food and quantity eaten, mg.		No. of eggs laid	Per cent of eggs hatching	Per cent of eggs dead
A. pisum	280	1600	63	26
A. fabae	220	75	45	48
R. maidis	200	680	71	27

Effects of Feeding on the Weight and Water Content of *C. maculata*

Sixty recently emerged and unfed adults of *C. maculata* were divided into five equal groups of 12 individuals. The adults of the first group were weighed individually and killed by freezing at −15° C. They were dehydrated and the dry weights were determined. The difference between the living and dry weights represented the water content. The adults were sexed using the characters of the internal genitalia. The insects of the second, third, fourth, and

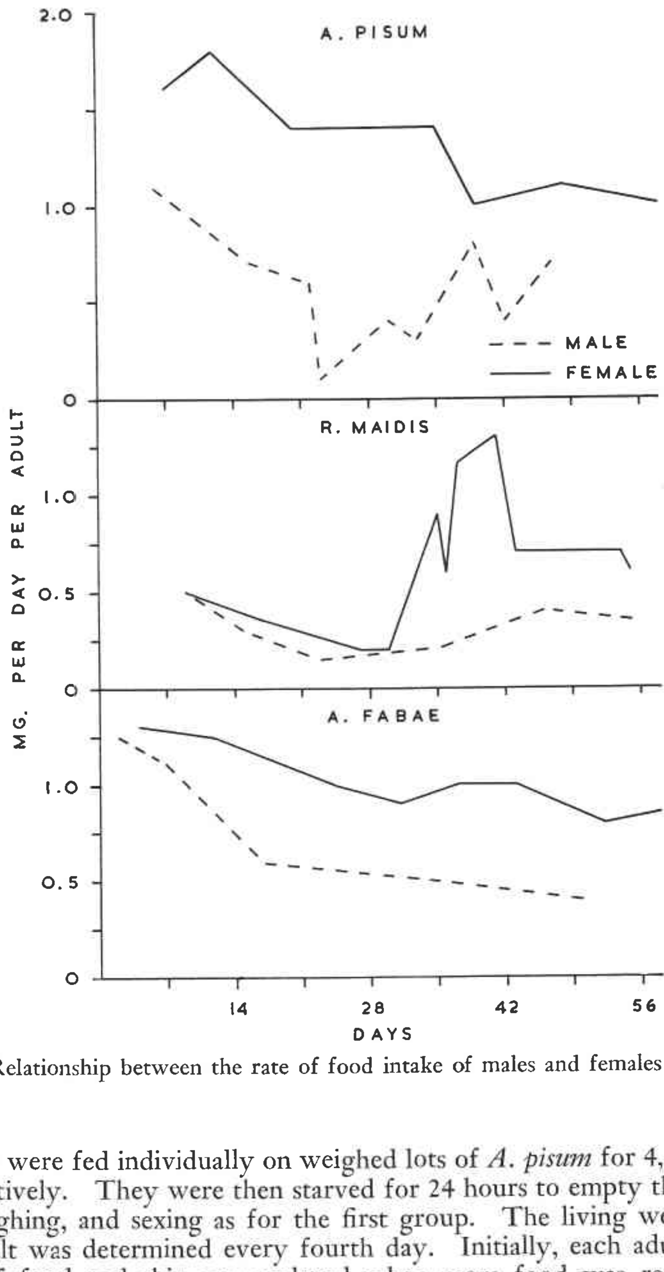

Fig. 3. Relationship between the rate of food intake of males and females of *C. maculata* and age.

fifth groups were fed individually on weighed lots of *A. pisum* for 4, 8, 12, and 28 days respectively. They were then starved for 24 hours to empty the gut before killing, weighing, and sexing as for the first group. The living weight of each feeding adult was determined every fourth day. Initially, each adult was given 10.0 mg. of food and this was replaced when more food was required. The quantity of food eaten in an interval was equal to the weight provided less the weight of the remaining food.

The indices of relative food intake, relative growth rate, and food efficiency were calculated from a number of measurements made on individuals and groups of adults. These were: the initial body weight, W1; the final body weight, W2; the quantity of food eaten, F; and the time of feeding, T. From these were calculated: the average body weight, $W = \frac{1}{2}(W1 + W2)$; the weight increase, $w = W2 - W1$; the index of relative food intake, F/TW; the index of relative growth, w/TW; and the index of food efficiency, w/F. The index of relative

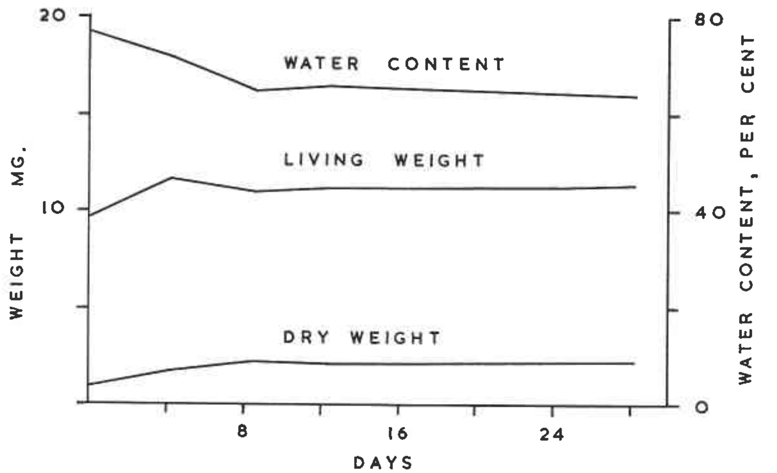

Fig. 4. Relationship between the water content and living and dry weights of *C. maculata* and age.

food intake was calculated for individuals as milligrams of food eaten per milligram of living adult per day. The indices of relative growth and of food efficiency were calculated for groups, the former as increase in dry weight of adult in milligrams per milligram of adult dry weight per day, and the latter as increase in dry weight of adult in milligrams per milligram of dry food eaten.

The living weight and the dry weight of feeding adults of *C. maculata* increased significantly during the first eight days and then did not vary, while the water content decreased significantly and then did not vary (Fig. 4). The dry weights of females were significantly greater than those of males in all groups. The index of food intake decreased during the first 15 days. After two, four, six, and 14 days it was 0.16 ± 0.01, 0.14 ± 0.01, 0.12 ± 0.01, and 0.09 ± 0.01 mg. per day respectively.

The index of relative growth was about 0.1 mg. per day during the first eight days and food efficiency was about 0.18 mg. per mg. of food. Sex had no effect on the three indices.

Conclusions

Females of *Coccinella trifasciata* are heavier and live longer than males. Longevity is 30% greater in females and 40% in males when drinking water is available than when it is not. Both sexes die when about one-third of the body water is lost. Water content is variable and is affected by the quality of the food. Adults lose water faster after eating food without protein than after eating food with protein. Availability of water and food quality probably interact in the field in their effects on the sex ratio and age distribution of an adult population.

Dry foods are more stable and can be handled and measured more easily than wet foods. The effects of dry, powdered foods on longevity and reproduction vary much both between and within species. Synthetic foods promote egg laying in *Coleomegilla maculata* but not in species of the genus *Coccinella.* Behavioural factors probably affect food intake and this and food utilization should be determined for each predator and food as some foods may not be digested. Food that is inadequate for egg production increases longevity, and in the field this kind of food may keep adults alive until food of higher quality is available. A diet based on desiccated liver is the most promising food supplement so far discovered for adults.

Previous feeding whether as larvae or as adults does not affect the preference of coccinellid adults. They prefer some foods to others and will eat foods not encountered in the field. *Anatis mali*, which is confined to conifers, will eat aphids grown on alfalfa and corn, i.e. *Acyrthosiphon pisum* and *Rhopalosiphum maidis*. Unpalatable aphids such as *Aphis fabae* are eaten when no better food is available. *C. maculata* prefers pollen to dry aphids, but the reason is unknown. A food supplement should not be more attractive to a predator than is its prey, but it should be sufficiently attractive to inhibit dispersion of the predator when prey are scarce. Supplementary foods will be most effective if used when coccinellid females are ovipositing and when young adults are present, as more food is eaten at those times.

When food is plentiful, *C. maculata* adults require about one week to mature. The food intake is higher during the first eight days after emergence than in older adults, and the water content decreases from 77 to 65%. The dry weight of the adult increases by about 100% with a food efficiency for growth of 18%. These changes may require a longer period of time when food is scarce. The dry weight and water content of an adult may be used to estimate the quantity and quality of food eaten.

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(Received 11 January 1965)