

FEEDING AND EGG PRODUCTION OF TWO SPECIES OF COCCINELLIDS IN THE LABORATORY

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Abstract

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The relationship between feeding rate and egg production of *Coccinella trifasciata* Mulsant and *C. californica* Mannerheim feeding on pea aphids, was investigated in the laboratory at 15.0°, 18.5°, 21.5°, and 25.5°C. Both species increase their feeding rate with increasing temperature above 13.6°C, with *C. californica*, the larger species, increasing its food consumption faster. *C. californica* also has the higher maintenance requirement but when food consumption is expressed relative to the beetles' body weight, there is no difference between the species in either attribute. *Coccinella californica* converts excess food to eggs more efficiently than *C. trifasciata*.

No significant influence of temperature on either the conversion rate or the maintenance requirement could be detected. The adverse effects of a very low feeding rate, whether due to restricted food supply or low temperature, influenced the beetles' response to subsequent treatments.

Introduction

This paper describes laboratory experiments on the influence of feeding on egg production by *Coccinella trifasciata* Mulsant and by *C. californica* Mannerheim, the two most common species of coccinellid in alfalfa in the Vancouver region.

Methods

Adults of *Coccinella trifasciata* and *C. californica* were collected from field alfalfa. In the laboratory each female was kept individually in a 3 cm diameter glass dish with a ground glass lid, provided with a two-ribbed piece of corrugated cardboard about 1 cm long in which to hide or lay eggs, and fed with adult pea aphids from a laboratory culture.

Three experimental feeding regimens were used: (1) a superabundance of food such that there was always at least one live aphid still intact by the next feeding time, (2) an intermediate quantity, and (3) a quantity barely exceeding that needed to keep the beetles alive (Table I). Experiments were performed at 15.0°, 18.5°, 21.5°, and 25.5°C. The numbers of beetles used in each particular treatment, and the treatment they had experienced immediately before it, are shown in Table II. Each day three samples each of 20 adult aphids from the culture, representative of those given as food, were weighed alive. The aphid remains for each beetle were collected cumulatively in an individual vial; at the end of the experiment they were dried and weighed. The dry-weight:wet-weight ratio of adult aphids from the culture was determined from a sample of 25. All eggs laid were removed and recorded when the beetles were fed.

At 21.5°C and 25.5°C the beetles were kept on a feeding regimen for about 10 days after most of them had begun to lay eggs, then moved to a different treatment. At 15.0°C and 18.5°C beetles were kept on any particular feeding regimen for 16 to 26 days on average. Beetles were weighed fully fed; those from treatments 2 and 3 were given a superabundance of food for 2 days after the treatment ended before they were weighed.

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Table I. Numbers of adult pea aphids fed daily to beetles in each treatment (mean aphid dry wt. consumed in treatments 2 and 3 is shown in parentheses. Dry wt. of 1 aphid = 0.53 mg)

Feeding treatment	15.0°C	18.5°C	21.5°C	25.5°C
	<i>C. californica</i>			
1*	2-5	8-15	12-24	22-40
2	-	-	6(3.18)	-
2	-	-	4(2.12)	4(2.12)
3	-	-	2(1.06)	3(1.59)
	<i>C. trifasciata</i>			
1*	2-4	4-8	6-16	9-35
2	1(0.53)	-	3(1.59)	5(2.65)
3	-	-	1(0.53)	2(1.06)

*In this treatment, beetles were given a superabundance of food. Thus the numbers of aphids given varied from beetle to beetle and from day to day, as explained in the text. The range in average numbers of aphids given per day is shown.

Eleven beetles were also used to observe long term egg production. Six *C. trifasciata* and five *C. californica*, all of which had experienced two feeding treatments at either 21.5°C or 25.5°C already, were kept at 21.5°C and fed a superabundance of aphids for a further 53-55 days, or until they died. Their food intake was not measured, but the number of eggs each beetle laid each day was recorded.

Results

Feeding rate. The wet-weight:dry-weight ratio of aphids differs between field and laboratory populations, so in this paper all feeding rates are expressed in mg dry weight eaten per day. In this case the wet-weight:dry-weight ratio was 5.0.

The feeding regimens 2 and 3, shortage of food, limited the beetles' feeding rate below their maximum (Table I). Only from regimen 1 could the relationship between temperature and maximum feeding rate be determined. Some beetles that were initially on low food treatments died before being fully fed and weighed. A crude estimate of the expected fully-fed weights of these beetles, predicted from the regression of fully-fed weight on abdomen width for all weighed beetles of the same species, enabled relative feeding rates to be calculated for most beetles.

When coccinellids are confined with a superabundant supply of aphids, as in feeding regimen 1, maximum feeding rate is a linear function of temperature (Figs. 1, 2). The regressions predict effective temperature thresholds for feeding at 13.6°C for both species. *C. californica*, the larger species, consumed more than *C. trifasciata* at temperatures above 13.6°C and increased its consumption faster than *C. trifasciata* for each degree rise in temperature (Fig. 1). But when the feeding rate is expressed relative to the beetles' body weight, there was no difference between the species (Fig. 2).

Egg production. The rate of egg production at a particular feeding rate depends both on a beetle's maintenance requirement (the x intercepts in Fig. 3) and on the rate of conversion of any further food to eggs (the regression slopes in Fig. 3). There were no significant differences between regression slopes or between intercepts at different temperatures (Table III, A).

We should naturally expect the metabolic rate, and therefore the daily maintenance requirement, to increase with temperature. Since the maintenance requirements at each temperature are estimated as the x -intercepts of regressions, they are inaccurate, especially at 15°C and 18.5°C where sample sizes were small. Although

Table II. Numbers of beetles in each treatment, and their immediately preceding treatment

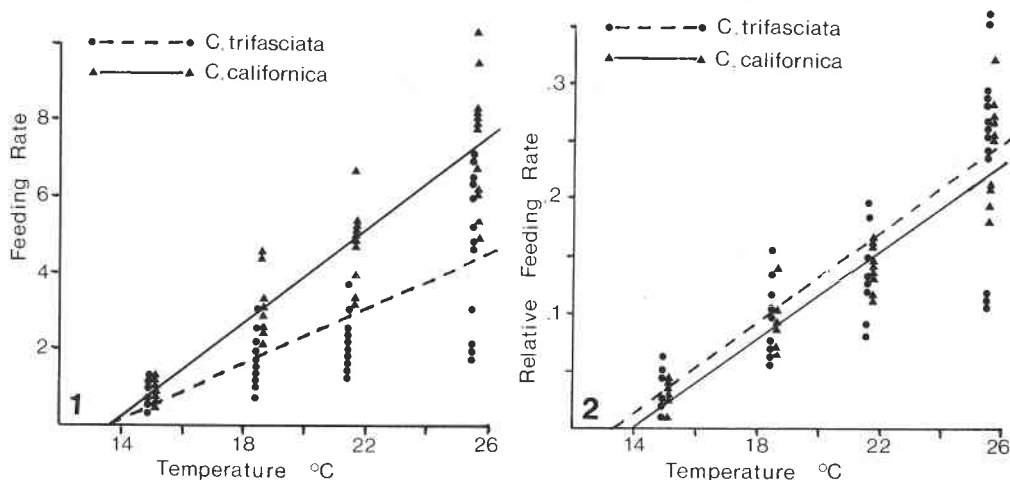
Current		Previous		No. of beetles	Total in current treatment
temp. (°C)	feeding treatment	temp. (°C)	feeding treatment		
<i>C. californica</i>					
15.0	1	-	-	9	9
18.5	1	21.5	3	6	8
18.5	1	15.0	1	2	
21.5	1	-	-	11	11
21.5	2	-	-	9	9
21.5	3	-	-	9	
21.5	3	21.5	1	11	29
21.5	3	21.5	2	9	
25.5	1	25.5	*	5	
25.5	1	21.5	3	5	12
25.5	1	15.0	1	2	
25.5	2	-	-	4	
25.5	2	21.5	3	1	6
25.5	2	15.0	1	1	
25.5	3	25.5	1	7	11
25.5	3	25.5	2	4	
<i>C. trifasciata</i>					
15.0	1	-	-	9	9
15.0	2	-	-	7	7
18.5	1	21.5	1	2	
18.5	1	21.5	2	2	10
18.5	1	21.5	3	3	
18.5	1	15.0	1	3	
21.5	1	-	-	10	10
21.5	2	-	-	10	10
21.5	3	-	-	8	
21.5	3	21.5	1	6	14
25.5	1	25.5	*	4	
25.5	1	21.5	1	1	
25.5	1	21.5	2	3	13
25.5	1	21.5	3	2	
25.5	1	15.0	1	3	
25.5	1	15.0	3	6†	
25.5	2	-	-	5	5
25.5	3	25.5	1	6	11
25.5	3	25.5	2	5	

*These beetles received a high and increasing quantity of food for several days (about a week) until the number of aphids required to provide a superabundance of food was found.

†These 6 beetles were excluded from the analyses due to detrimental effect of the previous treatment.

there is a tendency for daily maintenance requirement to increase with temperature (Table III, B), the increase is not significant. There is also a tendency for beetles to produce few eggs (low conversion rate) at low temperatures, but once again the differences are not significant. So the data from all four temperatures are adequately described by a single linear regression.

The adverse effects on the beetles of the lowest temperature (15°C) and the lowest feeding rate (regimen 3) continued beyond the end of those treatments into the treatment following: not only was the preoviposition period extended, but the beetles' maintenance requirement appeared to have increased. None of the other treatments had any effect on subsequent egg production. For seven of the 12



FIGS. 1-2. The influence of temperature (1) on the feeding rates (mg dry wt. of aphids eaten/beetle/day) and (2) on the relative feeding rates (mg dry wt. of aphids eaten/mg live beetle wt./day) of adult female *Coccinella trifasciata* and *C. californica*.

Table III, A. Estimated values for regressions of eggs laid/day on feeding rate; data for all four temperatures included, blocked by temperature (\pm S.E.)

	Absolute feeding rate	Relative feeding rate
<i>C. californica</i>		
mean body wt. (mg) 32.602 \pm 0.879		
Conversion rate	5.060 \pm 0.319	166.012 \pm 11.247
Maintenance requirement	1.055 \pm 0.162	0.034 \pm 0.005
r^2	0.726	0.717
Regression	$P < 0.001$	$P < 0.001$
Degrees of freedom of r^2	90	85
Between-block differences in:		
Conversion rates	N.S.	N.S.
Maintenance requirements	N.S.	N.S.
<i>C. trifasciata</i>		
mean body wt. (mg) 18.497 \pm 0.376		
Conversion rate	3.685 \pm 0.264	61.191 \pm 5.950
Maintenance requirement	0.741 \pm 0.116	0.037 \pm 0.009
r^2	0.707	0.576
Regression	$P < 0.001$	$P < 0.001$
Degrees of freedom of r^2	84	76
Between-block differences in:		
Conversion rates	N.S.	N.S.
Maintenance requirements	N.S.	N.S.

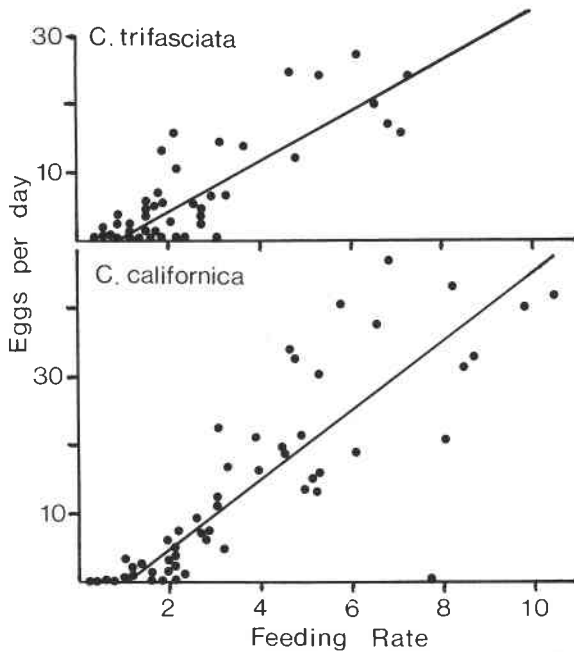


FIG. 3. The influence of absolute feeding rate (mg dry wt. of aphids eaten/beetle/day) on the rates of oviposition (eggs/female/day) by *Coccinella trifasciata* and *C. californica*.

C. californica and five of the 13 *C. trifasciata* tested at 25.5°C on feeding regimen 1, this treatment followed immediately upon either of 15°C or a feeding regimen 3 treatment. Likewise for all *C. californica* and six of the 10 *C. trifasciata* tested at 18.5°C, that treatment followed one or other of the two harsh treatments. The data are included in the analysis and in Fig. 3. But the results for six *C. trifasciata* that had been doubly stressed by reduced food (regimen 3) and temperature (15.0°C) before being placed at 25.5°C on feeding regimen 1, were omitted from the analysis due to the severe carryover effects.

Table III, B. Separate estimates, for each temperature, of the rate of conversion of excess food to eggs (regression slope) and the maintenance requirement (x -intercept)

Temp. (°C)	n	Absolute F.R.†		Relative F.R.†	
		C.R.*	M.R.*	C.R.	M.R.
<i>C. californica</i>					
15.0	9	3.281	0.696	35.992	.022
18.5	8	6.557	1.486	115.358	.003
21.5	49	5.393	1.049	178.171	.033
25.5	29	4.875	1.185	162.55	.042
<i>C. trifasciata</i>					
15.0	16	2.188	0.390	30.204	.018
18.5	10	3.137	1.25	38.073	.069
21.5	34	3.648	0.548	51.406	.024
25.5	29	3.717	0.923	64.866	.040

*C.R., conversion rate; M.R., maintenance requirement.

†F.R., feeding rates as defined in Fig. 1.

Species comparisons. As with the increase in maximum feeding rate with temperature, when food consumption is expressed relative to body weight the maintenance requirement differs little between the species (Table III, A). Each *C. californica* therefore requires more aphids per day for maintenance than each *C. trifasciata*; but when aphids are so abundant that *C. californica* can capture enough to exceed its maintenance requirement, this species converts excess food to eggs more efficiently than *C. trifasciata*.

Long term egg production. Most of the 11 beetles kept at 21.5°C for up to 55 days continued to lay eggs daily throughout the period, or until they died. In some there was a continuous very slow decline throughout the experiment, while others showed no consistent trend. Most beetles, however, did reduce their rate of egg production several days before death. Only one of the beetles failed to lay eggs at a high rate (≥ 20 or 30 eggs/day for *C. californica* and ≥ 10 or 15 eggs/day for *C. trifasciata*) for at least as many day-degrees as were accumulated between 1 May and 15 August, the potential period of coccinellid egg-laying in the field (Table IV).

Discussion

Although there have been numerous studies on feeding and reproduction in coccinellids, there have been few attempts to quantify the effects of temperature on the feeding rate of adult coccinellids (Gawande 1966), or the effects of adult feeding rate on oviposition (Ibrahim 1955), and none to relate these two effects.

The relationships reported here, determined in the laboratory with confined beetles, cannot by themselves predict egg production by coccinellids that must search for their prey. Frazer and Gilbert's (1976) field predation model for *C. trifasciata*, however, predicts feeding rate for any given temperature, aphid density, and coccinellid density. Thus it becomes possible to predict egg production by *C. trifasciata* in field cages and the open field. Relating the maintenance requirement of *C. trifasciata* (Table III, A) to Frazer and Gilbert's predation rate predicts that beetles of this species will be able to capture their maintenance requirement when the field density of pea aphids exceeds 0.3 aphid/stem, with an average age distribution. For *C. californica* the relationship between aphid density in the field, temperature and feeding rate has yet to be determined. Field observations suggest, however, that the searching efficiencies of the two species are not grossly different.

Both species of coccinellid occur and breed in the same alfalfa fields sharing the same prey, pea aphids. But the ratio of *C. trifasciata* to *C. californica* produced in an alfalfa field is not simply a function of the relative numbers of the two species in the parental generation. Rather, the ratio will depend on the history of aphid density and temperature, for the following reasons.

Table IV. Length of time (physiological) that beetles continued to lay eggs in the laboratory when provided with an abundance of aphids, compared with the potential egg-laying period in the field

In laboratory laying eggs	Day-degrees accumulated above the beetles' developmental threshold*:	
	In two field plots, May 1 to Aug 15*	
	Plot 1	Plot 2
Mean = 558.8	<i>C. californica</i>	
Range = 437-718		
Mean = 515.7	<i>C. trifasciata</i>	
Range = 449-656		

*Developmental thresholds, and field temperature data converted to day-degrees, both from Raworth, pers. comm.

Frazer *et al.* (this series) have found no differences in capture efficiency between same-aged larvae of the two species. But larger coccinellid larvae will eat eggs and smaller larvae if starving; larval development may be delayed by food shortage (Wratten 1973) exacerbating this cannibalism, and smaller larvae require a higher density of aphids to survive, even if not cannibalized (Wratten 1973, and this series). Thus the relative numbers of large, rather than total, larvae of the two species present when prey first become scarce, will determine the species ratio in survivors. *C. trifasciata* is advantaged by cool weather. *C. trifasciata* with its lower maintenance requirement can lay eggs at lower aphid densities than *C. californica*; if the aphids then increase sufficiently for the larvae to survive, *C. trifasciata* with its lower temperature threshold for development will have large larvae before *C. californica*. When aphids are abundant, however, *C. californica* can eat more of them, and converts excess food to eggs more efficiently than *C. trifasciata*; the warmer the weather, the greater is *C. californica*'s advantage.

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