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# Preimaginal Survival and Development of *Coleomegilla maculata* and *Hippodamia convergens* (Coleoptera: Coccinellidae) Reared on *Acyrtosiphon pisum*: Effects of Host Plants

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**ABSTRACT** *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* Guérin-Méneville larvae were supplied daily with  $\approx$ 1.2, 2.2, 4.3, 8.2, or 16.4 mg of *Acyrtosiphon pisum* Harris reared on either alfalfa *Medicago sativa* L. ('OK08') or faba beans *Vicia faba* L. ('Windsor'). Myristic acid and total fatty acid content ( $\mu\text{g}/\text{mg}$  aphid fresh weight) were 6.3 and 2.7 times greater, respectively, in pea aphids reared on alfalfa as compared with faba beans, resulting in a 1.17-fold increase in caloric content. Higher survival ratios were observed for both *C. maculata* and *H. convergens* supplied with low daily prey levels of pea aphids reared on alfalfa versus faba beans, but no differences were observed at higher prey levels. When pea aphids reared on alfalfa were supplied to *C. maculata* and *H. convergens* larvae at low prey levels, preimaginal developmental times were significantly reduced compared with those supplied with pea aphids reared on faba beans at the same prey levels. At higher daily pea aphid levels, *C. maculata* and *H. convergens* developmental times were not significantly different between host plants. At lower daily prey levels, *C. maculata* and *H. convergens* elliptical body area was larger when supplied with pea aphids reared on alfalfa, but body areas were similar at higher daily prey levels. Convergence of survival ratios, developmental times, and elliptical body areas for *C. maculata* and *H. convergens* at high (less limiting) prey levels supports the hypothesis that differences in prey nutritional value between pea aphids reared on alfalfa versus faba beans are quantitative and appear to be primarily influenced by differences in pea aphid myristic acid content.

**KEY WORDS** Coccinellidae, *Coleomegilla maculata*, *Hippodamia convergens*, *Acyrtosiphon pisum*, tritrophic interactions, fatty acids

BECAUSE PLANTS CAN affect third trophic level processes, understanding the interactions among plants, herbivores, and predators is necessary when predicting predator-prey relationships (Rice and Wilde 1989, van Emden and Wratten 1990, Faeth 1992, Obrycki and Kring 1998, Bottrell et al. 1998, Giles et al. 2000). Plants may influence predators through effects on herbivore population density, by altering prey capture, or by changing suitability of herbivorous prey (Price 1997). Chemical constituents of plants may result in toxic (antibiosis) or nutritionally unsuitable herbivorous prey, and may affect predator populations by increasing mortality, increasing developmental times, or reducing fecundity (Rice and Wilde 1989, Power 1992). Despite evidence that plants affect third trophic level processes, very few studies have investigated the mechanisms of these tritrophic interactions (Hodek and Honek 1996, Kareiva and Sahakian 1990, Giles et al. 2000).

Fatty acid content in pea aphids (*Acyrtosiphon pisum* Harris) varies with respect to host plant (Berg-

man et al. 1990, Dillwith et al. 1993, Giles et al. 2000). Pea aphids reared on alfalfa (*Medicago sativa* L. 'OK08') store significantly more energy in the form of triglycerides, as compared with those reared on faba beans (*Vicia faba* L. Windsor). Two- to six-fold increases in myristic acid content ( $\mu\text{g}/\text{mg}$  of aphid) are responsible for the increase in total fatty acid for pea aphids reared on alfalfa (Bergman et al. 1990, Neese 1995, Giles et al. 2000). This elevated myristic acid storage increases the caloric content of pea aphids reared on alfalfa and thus their nutritional value and may have an effect on the population dynamics of predators (Giles et al. 2000). For example, Bashir (1973) demonstrated that higher levels of myristic acid in artificial diets hasten larval development, increase size of adults, and increase fecundity of *Olla abdominalis* Say (Coleoptera: Coccinellidae).

Numerous studies have demonstrated that pea aphids are highly suitable prey for Coccinellidae (Smith 1965a, 1965b; Karner and Manglitz 1985; Phoolo and Obrycki 1997; Obrycki et al. 1997; Eigenbrode et al. 1998; Obrycki et al. 1998). However, little is known about how host plants can affect the nutritional value of pea aphids, and the subsequent effect on the preimaginal biology of Coccinellidae (Stockland

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2000). The goal of this study was to describe interactions among host plants (alfalfa or faba beans), pea aphid nutritional value (as influenced by changes in myristic acid storage), and the preimaginal biology of two coccinellid species. Specifically, we evaluated preimaginal survival and development, and growth (adult elliptical body area) of *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* (Guerin-Meneville) supplied with pea aphids reared on alfalfa or faba beans. *Hippodamia convergens* and *C. maculata* were chosen for this study because of their differences in prey specificity; *H. convergens* is primarily aphidophagous and *C. maculata* is polyphagous (Hodek and Honek 1996). This comparison in prey specificity may help to determine whether the observed differences in prey nutritional value, as influenced by host plants, has a greater effect on more prey-specific predators as opposed to more generalist predators.

We hypothesized that immature Coccinellidae predators would survive at higher rates, develop faster, and develop into larger adults when supplied with pea aphids from the alfalfa colony. That is, pea aphids from the alfalfa colony which stored significantly higher levels of energy (primarily as myristic acid) would be more suitable prey for Coccinellidae predators than pea aphids from the faba bean colony. By supplying Coccinellidae larvae a range of limiting (sub-optimal) daily prey levels (mg of pea aphids per day) from alfalfa or faba beans colonies, we were able to accurately compare suitability of aphids from separate host plants and simultaneously evaluate whether differences in prey nutritional value were quantitative or qualitative (Giles et al. 2000). Quantitative differences in prey nutritional value are simply differences in the total available useable nutrients (calories) as influenced by changes in nutritional energy sources such as myristic acid. Qualitative differences in prey nutritional value occur when less suitable prey lack essential nutrients or contain compounds, potentially derived from host plants, that may be toxic to predators. Quantitative differences in nutritional value of pea aphids reared on the two host plant species (alfalfa or faba beans) would be evident if survival, development, and growth of *C. maculata* and *H. convergens* differed at low (limiting) prey levels, but were similar at higher (less limiting) prey levels. If survival, development, and growth were different at both low and high daily prey levels, differences in the nutritional value of pea aphids between host plants would likely be qualitative.

### Materials and Methods

**Aphid and Coccinellid Colonies.** Pea aphids were reared on faba beans (*V. faba beans* L. Windsor) and used as the infestation source for an additional colony maintained on alfalfa (*M. sativa* OK08). These aphid colonies were maintained on their respective host plants in separate growth chambers at 22°C and a photoperiod of 16:8 (L:D) h.

Periodically during the experiment, late stage immature aphids (fourth nymphal stage) and apterous

adults were randomly collected from each pea aphid colony for nutritional evaluation. Following the standard methodology used by Bergman et al. (1991), analysis of fatty acid content was performed using gas chromatography on pea aphids collected from each colony (15–21 samples of 10-aphids) to measure variability within colonies. Caloric content of pea aphids was also quantified for each colony (three 5-g samples per colony) using an isoperibol calorimeter (model 1261, Parr Instruments, Moline IL). Protein content of pea aphids from each colony (three pooled 5-g samples from each colony) was quantified using proximate analysis (AOAC 1990).

Adult *C. maculata* and *H. convergens* were collected from North-central Oklahoma alfalfa fields. Twenty mating pairs of *C. maculata* and 16 mating pairs of *H. convergens* were maintained in half-pint cardboard ice cream containers with a fine mesh cover in an environmental chamber at 24°C and a photoperiod of 16:8 (L:D) h. Each pair was provided daily with an unlimited supply of pea aphids reared on faba beans, a moist cotton ball, and a supplementary diet of wheat-yeast-honey mixture.

**Feeding Studies.** Eggs from coccinellid mating pairs were collected daily, placed in 5-ml glass vials stopped with cotton and maintained in a table-top environmental chamber at 24°C and a photoperiod of 16:8 (L:D) h. Upon eclosion, larvae were placed individually in vials stopped with cotton and fed one of the following daily prey level treatments (mean  $\pm$  SE): two aphids ( $1.2 \pm 0.03$  mg), four aphids ( $2.2 \pm 0.06$  mg), seven aphids ( $4.3 \pm 0.12$  mg), 14 aphids ( $8.2 \pm 0.18$  mg), or 28 aphids ( $16.4 \pm 0.28$  mg) per day reared on alfalfa, or one aphid ( $1.2 \pm 0.06$  mg), two aphids ( $2.1 \pm 0.05$  mg), five aphids ( $4.3 \pm 0.09$  mg), 10 aphids ( $8.2 \pm 0.06$  mg), or 20 aphids ( $16.4 \pm 0.24$  mg) reared on faba beans. Only late stage immature pea aphids (fourth nymphal stage) and apterous adults were used as prey. Although numbers of prey provided from the two host plants differed, the daily prey levels (mg/d) were statistically similar between host plants at each prey level ( $F < 0.6$ ;  $df = 1, 48$ ;  $P > 0.473$ ). Approximately 16 mg (16.4) was chosen as the highest daily prey level because it represented an adequate diet for maximal development but is well below the daily consumption capabilities of late instar *C. maculata* and *H. convergens* (Obrycki and Orr 1990, Hodek and Honek 1996, Obrycki et al. 1998, Stockland 2000). During the study, late instar Coccinellidae consumed all available aphid prey (for each treatment) during each 24 h feeding interval. Thus, we controlled for the confounding effects of predator satiation, which allowed the effect of daily prey levels between host plants to be compared quantitatively. First instar coccinellids were occasionally unable to find and capture aphids when assigned to low daily prey levels. Therefore, to eliminate the potential effects of prey finding at the first instar, only Coccinellidae that fed on pea aphids and survived to the second instar were used for this study. A total of 54 individuals of each predator species was assigned to each daily prey level treat-

ment; coccinellid larvae from all parental lines were randomly assigned to all treatments.

Individual larvae were systematically checked each day to record mortality, molting, pupation, and adult emergence. Upon adult emergence, sex was determined, and body length and width were measured. Coccinellidae body length and width were used to calculate elliptical body area [ $\pi \times 1/2$  (body length)  $\times 1/2$  (body width)]. Elliptical body area represents the shape of an adult when viewed from above, and is closely correlated with adult weight (Obrycki et al. 1998).

**Statistical Analysis.** All analyses were performed using SAS version 6.12 for windows (SAS Institute 1996). A 0.05 significance level was chosen for all statistical analyses. Myristic acid and total fatty acid levels were compared between aphid colonies by analysis of variance (ANOVA) (PROC MIXED). The Mixed Procedure was used because it does not assume equal variances among treatments. We compared caloric content between aphid colonies by *t*-test (PROC *t*-test).

Ratios for larval survival, pupal survival, preimaginal survival, and sex were compared among treatments and between host plants using chi-square analysis (PROC FREQ) or Fisher exact test (two-tailed) when 50% of the cells had expected counts <5.

Developmental times (days) and adult body area (mm<sup>2</sup>) among treatments were analyzed by ANOVA (PROC MIXED). PROC MIXED was used because it supplies ANOVA with both random and fixed effects. Because parental line and sex may have been a source of experimental error, each were included in preliminary analyses as random factors. Data were subsequently pooled for analysis because no significant interactions were detected for sex of adults or parental line on developmental times or adult body area. Linear relationships between developmental times, adult body area and mg of aphids per day were analyzed by regression analysis (PROC GLM) for each host plant.

**Voucher Specimens.** Voucher specimens (*C. maculata* and *H. convergens* adults) are deposited in the Department of Entomology and Plant Pathology museum at Oklahoma State University, Stillwater.

## Results

**Pea Aphid Colonies.** There were significant differences between aphid colonies in total fatty acid ( $F = 30.2$ ;  $df = 1, 34$ ;  $P < 0.001$ ) and myristic acid ( $F = 37.9$ ;  $df = 1, 34$ ;  $P < 0.001$ ) content (Table 1). *Acyrtosiphon pisum* reared on alfalfa had an average ( $\pm$ SE) total fatty acid content of  $17.96 \pm 1.32$   $\mu$ g/mg (fresh weight) and an average myristic acid content of  $12.62 \pm 1.09$   $\mu$ g/mg. The average total fatty acid and myristic acid content for aphids reared on faba beans was  $6.59 \pm 1.56$  and  $2.01 \pm 1.29$   $\mu$ g/mg, respectively. The caloric content of pea aphids also varied significantly between colonies ( $t = 4.9$ ,  $df = 4$ ,  $P = 0.008$ ). The average ( $\pm$ SE) calories per mg of fresh aphid weight for aphids reared on alfalfa and faba beans were  $1.195 \pm 0.009$  and  $1.021 \pm 0.029$ , respectively.

**Table 1.** Daily pea aphid prey level treatments, estimated myristic and fatty acid content, and caloric content for each treatment

Host plant	Pea aphids mg/day $\pm$ SE <sup>a</sup>	Myristic acid content ( $\mu$ g) <sup>b</sup>	Fatty acid content ( $\mu$ g) <sup>b</sup>	Calories <sup>c</sup>
Alfalfa	1.2 $\pm$ 0.03	15.1	21.5	1.434
Faba bean	1.2 $\pm$ 0.06	2.4	7.9	1.225
Alfalfa	2.2 $\pm$ 0.06	28.7	39.6	2.629
Faba bean	2.1 $\pm$ 0.05	4.3	13.8	2.143
Alfalfa	4.3 $\pm$ 0.12	54.3	77.2	5.138
Faba bean	4.3 $\pm$ 0.09	8.6	28.3	4.388
Alfalfa	8.2 $\pm$ 0.18	103.5	147.3	9.799
Faba bean	8.2 $\pm$ 0.06	16.5	54.0	8.369
Alfalfa	16.4 $\pm$ 0.28	207.0	294.6	19.597
Faba bean	16.4 $\pm$ 0.24	33.0	108.1	16.737

<sup>a</sup> Daily prey levels (mg/day) were statistically similar between host plants at each prey level ( $F < 0.6$ ;  $df = 1, 48$ ;  $P > 0.473$ ).

<sup>b</sup> Estimated from results of lipid analysis ( $\mu$ g/mg aphid).

<sup>c</sup> Calories estimated from result of bomb calorimetry.

Between colonies, percent protein was nearly identical; aphids reared on alfalfa contained 10.9% protein, whereas aphids reared on faba beans contained 10.6% protein.

**Survival and Sex Ratio.** Larval, pupal and preimaginal survival ratios for *C. maculata* increased before plateauing across the 8.2 and 16.4 mg daily prey levels (Table 2). There were significant differences in *C. maculata* pupal ( $\chi^2 = 8.472$ ,  $df = 1$ ,  $P = 0.004$ ) and preimaginal ( $\chi^2 = 8.704$ ,  $df = 1$ ,  $P = 0.003$ ) survival between host plants at the 1.2 mg daily prey level (Table 2). Survivorship of *C. maculata* was higher for larvae supplied with pea aphids from the alfalfa colony.

Larval, pupal and preimaginal survival ratios for *H. convergens* increased before plateauing between the 8.2 and 16.4 mg prey levels (Table 2). There were significant differences between host plants for *H. convergens*, larval, pupal and preimaginal survival at the 1.2 mg daily prey level ( $\chi^2 = 37.1$ ,  $df = 1$ ,  $P < 0.001$ ;  $\chi^2 = 8.9$ ,  $df = 1$ ,  $P = 0.003$ ;  $\chi^2 = 33.7$ ,  $df = 1$ ,  $P < 0.001$ , respectively), and significant differences in larval and preimaginal survival at the 2.1 or 2.2 mg prey levels ( $\chi^2 = 7.1$ ,  $df = 1$ ,  $P = 0.008$ ;  $\chi^2 = 7.8$ ,  $df = 1$ ,  $P = 0.005$ , respectively; Table 2). Similar to *C. maculata*, survivorship of *H. convergens* was higher for larvae supplied with pea aphids from the alfalfa colony.

For each coccinellid species, a significant difference in the ratio of females was detected among prey levels ( $\chi^2 > 17.0$ ,  $df = 4$ ,  $P < 0.002$ ), however there were no significant differences between host plants at any one prey level (Table 2).

**Development.** For *C. maculata*, larval and preimaginal developmental times were significantly different among daily prey levels and between host plants, and the interaction between host plants and daily prey level was significant (Table 3; Fig. 1). However, pupal developmental times (days  $\pm$  SE), which ranged from  $4.3 \pm 0.2$ – $5.1 \pm 0.3$ , were not significantly different among daily prey levels or between host plants (Table 3). Significant nonlinear (quadratic) relationships between decreasing developmental times for *C. maculata* and increasing prey levels were detected for both

**Table 2.** Survival and female ratios for *C. maculata* and *H. convergens* at 24°C and a photoperiod of 16:8 (L:D) h when supplied with increasing daily levels of pea aphids reared on alfalfa or faba beans

Variable	Daily prey level of pea aphids (mg/day) from each host plant									
	1.2		2.2		4.3		8.2		16.4	
	Alfalfa <sup>a</sup>	Faba <sup>b</sup>	Alfalfa	Faba	Alfalfa	Faba	Alfalfa	Faba	Alfalfa	Faba
<i>C. maculata</i>										
Larval survival	0.556	0.444	0.944	0.870	0.981	0.963	1.000	1.000	0.926	0.981
Pupal survival	0.767	0.375*	0.784	0.915	0.924	0.981	0.888	0.944	0.940	1.000
Preimaginal survival	0.426	0.167*	0.741	0.796	0.907	0.944	0.889	0.944	0.870	0.981
Female ratio	0.364	0.222	0.375	0.200	0.614	0.449	0.576	0.721	0.767	0.717
n	54	54	54	54	54	54	54	54	54	54
<i>H. convergens</i>										
Larval survival	0.889	0.315*	0.981	0.833*	0.944	0.926	0.981	0.944	0.944	0.981
Pupal survival	0.708	0.294*	0.774	0.600	0.804	0.920	0.962	0.922	0.922	0.981
Preimaginal survival	0.630	0.093*	0.759	0.500*	0.759	0.852	0.944	0.870	0.870	0.963
Female ratio	0.303	0	0.158	0.111	0.281	0.333	0.636	0.550	0.868	0.705
n	54	54	54	54	54	54	54	54	54	54

\* Paired values represent significant differences ( $P < 0.05$ ) for  $2 \times 2$  chi-square tests between host plants. n, total number of pea aphids per treatment at beginning of experiment.

<sup>a</sup> Pea aphids reared on alfalfa.

<sup>b</sup> Pea aphids reared on faba bean.

alfalfa (larval:  $r^2 = 0.561$ ;  $df = 1, 192$ ;  $P < 0.001$ ; preimaginal:  $r^2 = 0.506$ ;  $df = 1, 200$ ;  $P < 0.001$ ) and faba beans (larval:  $r^2 = 0.713$ ;  $df = 1, 182$ ;  $P < 0.001$ ; preimaginal:  $r^2 = 0.600$ ;  $df = 1, 202$ ;  $P < 0.001$ ; Fig. 1).

Larval developmental times were significantly reduced for *C. maculata* supplied with pea aphids reared on alfalfa versus faba beans at the 1.2 mg ( $F = 40.7$ ;  $df =$

1, 354;  $P < 0.001$ ), 2.1 or 2.2 mg ( $F = 15.7$ ;  $df = 1, 354$ ;  $P < 0.001$ ) and 16.4 mg ( $F = 4.5$ ;  $df = 1, 354$ ;  $P = 0.034$ ) daily prey levels (Fig. 1A). The observed difference in larval developmental time at the 16.4 mg daily prey level reflect  $\approx 1$  d difference between aphid source (host plant), compared with  $\approx 4.2$  d difference at 1.2 mg. Preimaginal developmental times were shorter for

**Table 3.** ANOVA results (Mixed Procedure, SAS) for *C. maculata* and *H. convergens* developmental times (days) and adult elliptical body area reared on increasing daily prey levels of pea aphids from alfalfa and faba beans

	Source of variation	Tests of fixed effects		
		df <sup>a</sup>	F	P
<i>C. maculata</i>				
Larval development	Host plant	1, 354	50.72	<0.001
	Prey level	4, 354	265.66	<0.001
	Host plant $\times$ Prey level	4, 354	6.39	<0.001
Pupal development	Host plant	1, 384	0.26	0.608
	Prey level	4, 384	0.74	0.563
	Host plant $\times$ Prey level	4, 384	0.71	0.582
Preimaginal development	Host plant	1, 384	45.55	<0.001
	Prey level	4, 384	147.63	<0.001
	Host plant $\times$ Prey level	4, 384	5.13	<0.001
Adult body area (mm <sup>2</sup> ) <sup>b</sup>	Host plant	1, 349	4.56	0.033
	Prey level	4, 349	75.89	<0.001
	Host plant $\times$ Prey level	4, 349	6.72	<0.001
<i>H. convergens</i>				
Larval development	Host plant	1, 386	228.99	<0.001
	Prey level	4, 386	430.19	<0.001
	Host plant $\times$ Prey level	4, 386	27.51	<0.001
Pupal development	Host plant	1, 366	0.71	0.401
	Prey level	4, 366	1.55	0.188
	Host plant $\times$ Prey level	4, 366	1.81	0.126
Preimaginal development	Host plant	1, 367	14.69	<0.001
	Prey level	4, 367	188.32	<0.001
	Host plant $\times$ Prey level	4, 367	1.48	<0.001
Adult body area (mm <sup>2</sup> ) <sup>a</sup>	Host plant	1, 333	14.69	<0.001
	Prey level	4, 333	188.32	<0.001
	Host plant $\times$ Prey level	4, 333	1.48	0.209

Host plants were alfalfa and faba beans. Daily prey levels from alfalfa were (mean  $\pm$  SE) 1.2  $\pm$  0.03, 2.2  $\pm$  0.06, 4.3  $\pm$  0.12, 8.2  $\pm$  0.18, or 16.4  $\pm$  0.28 mg/day of pea aphids. The daily prey levels from faba beans were (mean  $\pm$  SE) 1.2  $\pm$  0.06, 2.1  $\pm$  0.05, 4.3  $\pm$  0.09, 8.2  $\pm$  0.06, or 16.4  $\pm$  0.24 mg.

<sup>a</sup> Additional replications represent accurate measures on adult emergence but with missing data on larval developmental times.

<sup>b</sup> Calculated using equation for an ellipse [ $\pi \times 1/2$  (body length)  $\times$  1/2 (body width)].

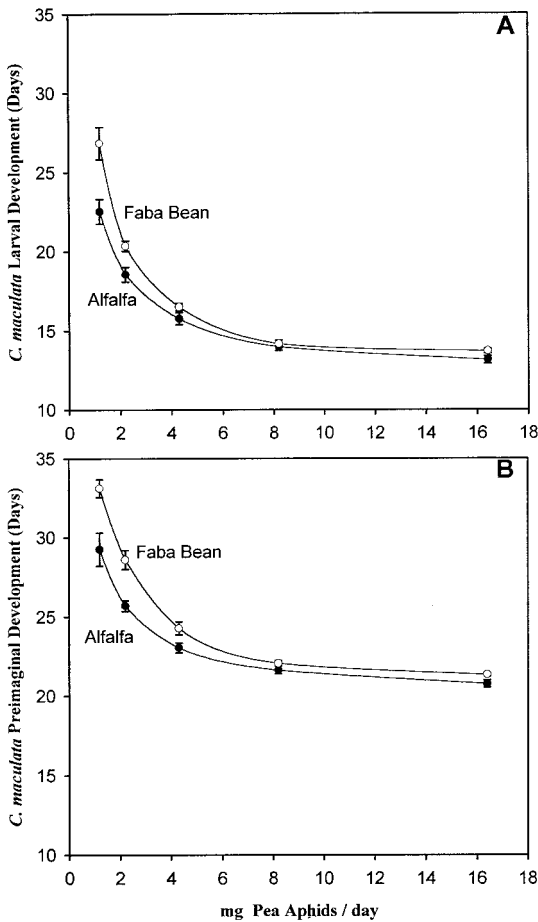


Fig. 1. Mean developmental times  $\pm$  SE for *C. maculata* at 24°C and a photoperiod of 16:8 (L:D) h when supplied with increasing daily levels of pea aphids reared on alfalfa (●) or faba bean (○). Developmental times are shown for larval (A) and preimaginal (B) stages.

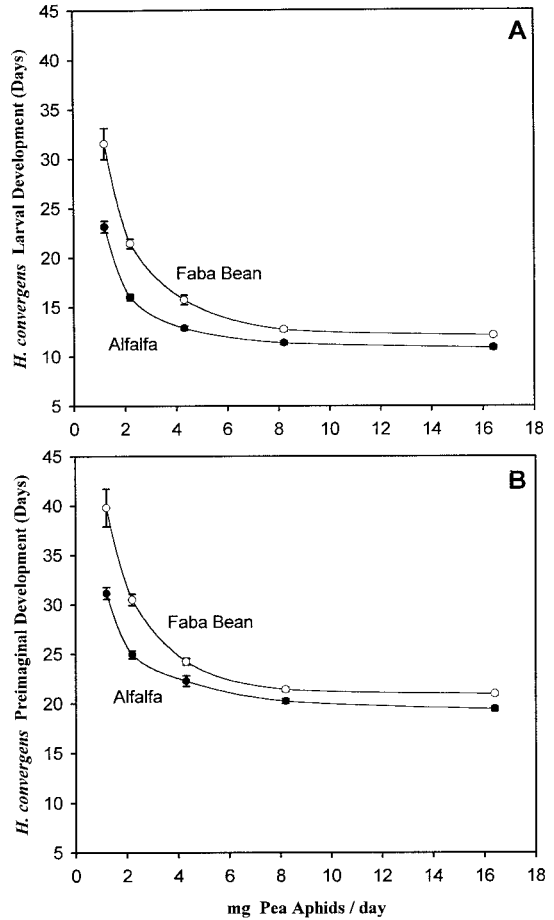


Fig. 2. Mean developmental times  $\pm$  SE for *H. convergens* at 24°C and a photoperiod of 16:8 (L:D) h when supplied with increasing daily levels of pea aphids reared on alfalfa (●) or faba bean (○). Developmental times are shown for larval (A) and preimaginal (B) stages.

*C. maculata* supplied the 1.2 mg ( $F = 17.2$ ;  $df = 1, 384$ ;  $P < 0.001$ ), 2.1 or 2.2 mg ( $F = 130.4$ ;  $df = 1, 384$ ;  $P < 0.001$ ) and 4.3 mg ( $F = 6.7$ ;  $df = 1, 384$ ;  $P = 0.010$ ) daily prey levels with aphids from alfalfa (Fig. 1B). The observed difference in preimaginal developmental time at the 1.2 mg daily prey level reflects  $\approx 3.9$  d difference between aphid host plant.

For *H. convergens* supplied with pea aphids reared on either alfalfa or faba beans, larval and preimaginal developmental times were different among daily prey levels and between host plants and interactions among host plants and daily prey levels were significant (Table 3; Fig. 2). Pupal developmental times (days  $\pm$  SE), which ranged from  $5.2 \pm 0.2$  to  $6.1 \pm 0.3$ , were not significantly different among daily prey levels or between host plants (Table 3). There was a significant nonlinear relationship between decreasing developmental times and increasing prey levels for both alfalfa (larval:  $r^2 = 0.669$ ;  $df = 1, 218$ ;  $P < 0.001$ ; preimaginal:  $r^2 = 0.622$ ;  $df = 1, 211$ ;  $P < 0.001$ ) and faba (larval:  $r^2 =$

$0.685$ ;  $df = 1, 187$ ;  $P < 0.001$ ; preimaginal:  $r^2 = 0.703$ ;  $df = 1, 174$ ;  $P < 0.001$ ; Fig. 2).

At all daily prey levels, larval ( $F > 4.6$ ;  $df = 1, 386$ ;  $P < 0.033$ ) and preimaginal ( $F > 5.0$ ;  $df = 1, 367$ ;  $P < 0.026$ ) developmental times were significantly shorter for *H. convergens* supplied with pea aphids reared on alfalfa versus faba beans (Fig. 2). The observed difference in larval and preimaginal developmental time at the 16.4 mg daily prey level reflect  $\approx 1.1$  d and 1.2 d differences between aphid source (host plant), compared with  $\approx 8.7$  d and 8.9 d differences at 1.2 mg.

**Adult Elliptical Body Area.** For *C. maculata* supplied with pea aphids reared on alfalfa or faba beans, adult elliptical body area ( $\text{mm}^2$ ) significantly differed between host plants and among daily prey levels, and a significant interaction between daily prey level and host plants was detected (Table 3; Fig. 3A). There were significant but weak nonlinear (quadratic) relationships between increasing body area for *C. maculata* and increasing prey levels for alfalfa ( $r^2 = 0.299$ ;

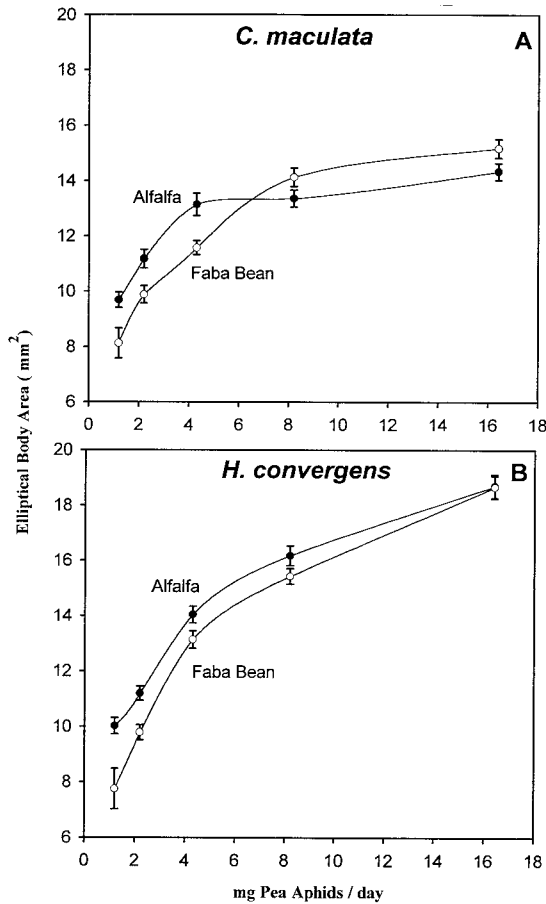


Fig. 3. Mean  $\pm$  SE elliptical body area for *C. maculata* (A) and *H. convergens* (B) at 24°C and a photoperiod of 16:8 (L:D) h when supplied with increasing daily levels of pea aphids reared on alfalfa (●) or faba bean (○). Body area was calculated using equation for an ellipse [ $\pi \times 1/2$  (body length)  $\times$  1/2 (body width)].

df = 1, 182;  $P < 0.001$ ) and faba beans ( $r^2 = 0.530$ ; df = 1, 195;  $P < 0.001$ ; Fig. 3A). Body area was significantly larger for *C. maculata* supplied with pea aphids reared on alfalfa at the 2.1 or 2.2 mg and 4.3 mg daily prey levels ( $F > 6.9$ ; df = 1, 349;  $P < 0.009$ ; Fig. 3A).

For *H. convergens* supplied with pea aphids reared on alfalfa or faba beans, adult elliptical body area (mm<sup>2</sup>) significantly differed between host plants and among daily prey levels; however, a significant interaction between daily prey level and host plants was not detected (Table 3; Fig. 3B). There was a significant nonlinear relationship between increasing body area for *H. convergens* and increasing prey levels for alfalfa ( $r^2 = 0.667$ ; df = 1, 200;  $P < 0.001$ ) and faba beans ( $r^2 = 0.685$ ; df = 1, 155;  $P < 0.001$ ). Body area was larger for *H. convergens* supplied with pea aphids reared on alfalfa at the 1.2 mg, 2.1 or 2.2 mg and 4.3 mg daily prey levels ( $F > 3.8$ ; df = 1, 333;  $P < 0.049$ ; Fig. 3B).

Discussion

Low daily prey levels and consumption of less suitable aphid prey during larval stages can result in lower survival, longer developmental times, and decreased weight and size of Coccinellidae (Smith 1965c, 1965d; Baumgaertner et al. 1981; Mills 1981; Hodek and Honek 1996; Phoofole and Obrycki 1997; Obrycki et al. 1998). In this study, lower prey levels resulted in reduced survival of both *C. maculata* and *H. convergens*. Our results for *C. maculata* preimaginal survivorship fed suboptimal quantities compare closely with those of Obrycki et al. (1998), who also observed decreasing survivorship when daily levels of pea aphids were reduced. *Coleomegilla maculata* fed the 1.2-mg daily prey level had significantly higher preimaginal survival when provided aphids from alfalfa versus faba bean; there were no significant differences at higher prey levels. Similarly, *H. convergens* supplied daily with 1.2–2.2 mg of aphids reared on alfalfa had significantly higher larval and preimaginal survival compared with larvae fed aphids reared on faba beans. Host plant did not significantly affect the survival of *H. convergens* at the higher prey levels (Table 2). Convergence of survival ratios as prey levels from each host plant increase for both *C. maculata* and *H. convergens* suggests that differences in survival can be attributed to quantitative differences in the nutritional value of prey.

For both coccinellid species, host plant had no effect on female ratios (Table 2). Female ratios did decline, however, as daily prey levels decreased, indicating increased survivorship of males at low prey densities (Table 2). Smith (1965b) observed a similar reduction in the proportion of surviving *C. maculata* females supplied with limiting levels of dried pea aphids. The reduced female ratios at low prey levels were attributed to greater food requirements for females compared with males.

We observed a nonlinear (quadratic) relationship between decreasing prey levels and developmental times for both *C. maculata* and *H. convergens*. Similarly, for *Adalia bipunctata* L. developmental rates increased nonlinearly as food levels increased (Mills 1981). For *C. maculata* reared on aphids from either alfalfa or faba beans, the minimum preimaginal developmental time occurs when supplied between 8.2 and 16.4 mg fresh weight of prey per day, whereas for *H. convergens* it is at least 16.4 mg of aphids per day (Figs. 1 and 2). The minimum developmental times reported in our study compare closely with previously reported values for *C. maculata* and *H. convergens* (Smith 1965c, Obrycki and Tauber 1978, Obrycki and Tauber 1982, Obrycki et al. 1998).

The significant decreases in larval and preimaginal developmental times at the lower prey levels for *C. maculata* and *H. convergens* fed pea aphids reared on alfalfa indicate a host plant effect on the third trophic level. The minimum preimaginal developmental times for *C. maculata* and *H. convergens* reflect approximately a 1-d difference between host plants (16.4 mg prey level; Figs. 1B and 2B). At the 1.2-mg daily prey

level, *C. maculata* and *H. convergens* preimaginal developmental times between host plants were  $\approx 4$  and 9 d apart, respectively. The different responses between the two species may be due to differences in food specificity; *C. maculata* is highly polyphagous and may be more capable of assimilating a broader range of prey nutrients compared with the primarily aphidophagous *H. convergens* (Hodek and Honek 1996). Preimaginal developmental times at the higher prey levels were statistically similar for *C. maculata*, suggesting that quantitative nutritional differences between pea aphid colonies and not host plant derived antibiosis are causing differences in developmental times for those fed the lower daily prey levels. Additionally, significant convergence of development at high prey levels (significant interaction between host plant and daily prey level) further supports this conclusion (Fig. 1B). For *H. convergens* larval and preimaginal development, host plant did have a significant effect for all prey levels (Fig. 2B). However, similar to *C. maculata*, the differences in developmental times still converged (significant interactions) between host plants at the higher daily prey levels, suggesting that the differences in developmental time for *H. convergens* can be attributed to quantitative differences in nutritional value of prey.

The size of adult coccinellids may significantly influence subsequent populations; Sundby (1968) demonstrated that smaller females are less fecund. Adult elliptical body area was significantly larger for both *H. convergens* and *C. maculata* larvae supplied low daily levels of pea aphids (during the larval stage) reared on alfalfa, as opposed to those supplied with aphids reared on faba beans. Body area is statistically similar between host plants at the higher daily prey levels, again suggesting that the differences in body area for both *C. maculata* and *H. convergens* can be attributed to quantitative differences in nutritional value of prey. Linear relationships between prey consumption and growth have been well documented for insect predators, including Coccinellidae (Mills 1981, Baumgaertner et al. 1981). In this study, adult elliptical body area increased nonlinearly (quadratically) with increasing levels of prey. However, adult body size is often determined by factors other than prey consumption and nutrient assimilation (Smith 1965d, Hodek and Honek 1996). For example, Rodriguez-Saona and Miller (1990) found that *H. convergens* reared at different temperatures varied in body size; adults reared at 18 and 22°C were significantly larger than those reared at 26 and 30°C (Rodriguez-Saona and Miller 1990).

Pea aphids store energy in the form of tryglycerides, primarily as myristic acid which is a 14-carbon saturated fatty acid (Dillwith et al. 1993). Fatty acids, such as myristic acid, are used as energy sources by aphidophagous predators (Kaplan et al. 1986, Baumgaertner et al. 1981, Bashir 1973). The differences in myristic acid content between aphids reared on alfalfa and faba beans provide significant nutritional differences to both *H. convergens* and *C. maculata*. A greater than six-fold increase in myristic acid for pea aphids reared

on alfalfa is responsible for the 2.7-fold increase in fatty acids and a resulting 1.17-fold increase in calories (Table 1). These differences in myristic acid levels, and subsequent quantitative differences in the nutritional value of pea aphids between host plants, appear to affect the survival, development and size of *C. maculata* and *H. convergens*. Convergence of survivorship, developmental times and adult body area at high (less limiting) daily pea aphids levels supports this hypothesis. Additionally, a similar response has been observed for *Coccinella septempunctata* L. supplied with limiting daily pea aphid levels; preimaginal development times (between host plants) were different at low prey levels but converged at higher daily pea aphid levels, and appear to be primarily influenced by differences in myristic acid content (Giles et al. 2001). The quantitative nutritional effects of increased myristic acid levels on Coccinellidae have been previously demonstrated with artificial diets. In a laboratory study, Bashir (1973) demonstrated that increased levels of myristic acid in artificial diets decreased developmental times and increased adult size of *O. abdominalis*. These results, however, are not consistent for all aphidophagous predators feeding on pea aphids. When *Chrysoperla rufilabris* Burmeister were supplied with pea aphids from alfalfa or faba bean colonies, developmental rates diverged at higher daily pea aphid levels (Giles et al. 2000). Clearly, the factors that influence tritrophic interactions can be quite different among aphidophagous predators.

The indirect effect of host plant on the preimaginal biology of *C. maculata* and *H. convergens* was clearly demonstrated at low (limiting) prey daily prey levels, but not at higher (less limiting) daily prey levels. Additionally, our study supports the hypothesis that quantitative differences in the nutritional value of pea aphids as determined by differences in myristic acid content between aphids reared on alfalfa versus faba beans affect *C. maculata* and *H. convergens* survival, developmental times and adult body area. Detailed quantification of amino acid levels and concentrations of essential minerals within pea aphids, and experimental studies using artificial diets will aid in identifying the role of other nutritionally important molecules for *C. maculata* and *H. convergens*. Future studies designed to evaluate the role of pea aphid nutritional value (between host plants) on *C. maculata* and *H. convergens* reproduction will provide additional insights toward identifying the role of myristic acid on Coccinellidae population dynamics.

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