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Quantitative evaluation of suitability of the greenbug, *Schizaphis graminum*, and the bird cherry-oat aphid, *Rhopalosiphum padi*, as prey for *Hippodamia convergens* (Coleoptera: Coccinellidae)

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Abstract

The nutritive value of two cereal aphid species, *Schizaphis graminum* and *Rhopalosiphum padi*, for *Hippodamia convergens* development was compared as pure- and mixed-species diets and as suboptimum and *ad libitum* quantities. Comparisons were based on the following daily aphid quantities and combinations: 4 mg *R. padi*, 4 mg *S. graminum*, 3:1 mg mixture of *R. padi* and *S. graminum*, 2:2 mg mixture of *R. padi* and *S. graminum*, 1:3 mg mixture of *R. padi* and *S. graminum*, *ad libitum R. padi*, and *ad libitum S. graminum*. Preimaginal survival levels of *H. convergens* were high across all treatments and were neither influenced by aphid species, daily amounts of aphids, nor the mixtures supplied to the larvae. There was no diet effect on the sex ratio of individuals that developed to adulthood. Only the development time of fourth instars was significantly influenced by the larval prey regimes. Fourth instars fed *ad libitum* aphids had shorter development times that did not vary between aphid species. However, among the suboptimal aphid levels, fourth instars that fed on higher proportions of *R. padi* had longer development times. Both diet and gender of developing larvae had individual and interactive effects on the body size of adult *H. convergens*. Under *ad libitum* aphids feeding on *R. padi* resulted in smaller females whereas males showed no difference. Our results suggest that both *R. padi* and *S. graminum* are essential prey for *H. convergens* development with *S. graminum* being relatively more suitable than *R. padi*.

Keywords: *Schizaphis graminum*; *Rhopalosiphum padi*; *Hippodamia convergens*; Suboptimal prey levels; Cereal aphids; Predator; Prey suitability; Nutritive value; Biological control

1. Introduction

Hippodamia convergens Guerin-Meneville (Coleoptera: Coccinellidae) is one of the dominant aphidophagous ladybeetle species in many agroecosystems throughout the Nearctic region (Gordon, 1985; Kring et al., 1985; Rice and Wilde, 1988; Elliott and Kieckhefer, 2000; Mohammed et al., 2000; Michels et al., 2001). In the Great Plains of the United States *H. convergens* consistently co-occurs with the greenbug, *Schizaphis graminum* (Rondani) (Homoptera: Aphididae) and the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Homoptera: Aphididae). Both species are two of the most abundant and widely distributed aphids in Great Plains wheat production systems (Feng et al., 1992; Wraight et al., 1993; Schotzko and Bosque-Perez, 2000). It can therefore be expected that, as a result of this simultaneous occurrence, *H. convergens* not only encounters these cereal aphids frequently but that they also comprise a large proportion of the beetle's prey in wheat agroecosystems.

Several studies have shown that although different aphid species can be accepted or consumed by a predator, their relative suitability can vary drastically (Hodek and Honek, 1996; Kalushkov and Hodek, 2001; Işikber and Copland, 2002; Özder and Sağlam, 2003). Ranking of aphids, based on their suitability as prey for ladybeetles, ranges from

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essential prey to alternative prey (Hodek and Honek, 1996). Essential prey species are those that ensure complete and fast preimaginal development, low mortality, larger body size, and high fecundity, whereas alternative prey species only provide nutrients that sustain survival longer than it would otherwise be possible under starvation (Hodek and Honek, 1996; Kalushkov and Hodek, 2001; Işikber and Copland, 2002; Özder and Sağlam, 2003; Michaud, 2005).

Unlike the greenbug, which has been demonstrated experimentally to be an essential prey for *H. convergens* (e.g., Michels and Behle, 1991; Formusoh and Wilde, 1993), the suitability of bird cherry-oat aphid for this ladybeetle has not been (experimentally) evaluated. Most studies that evaluated prey suitability of bird cherry-oat aphid on other predator species indicate that, although it qualified as an essential prey, it was of lower nutritional value than other cereal aphids. For example, bird cherry-oat aphid was found to be less suitable than *Sitobion avenae* (F.) and *Metopolophium dirhodum* (Walker) as prey for both specialist and generalist aphid predators (Toft, 1995; Hauge et al., 1998; Jørgensen and Toft, 1997; Bilde and Toft, 1999; Toft, 2000; Kyneb and Toft, 2004). The specialist aphid predator used in these studies was *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) (Hauge et al., 1998) whereas generalist predators included carabids (Jørgensen and Toft, 1997; Bilde and Toft, 1999), staphylinids (Kyneb and Toft, 2004), and spiders (Toft, 2000). There is also an indication that bird cherry-oat aphid might be toxic to predators, as it has been shown to induce production and activity of detoxifying enzymes by *C. septempunctata* (Nielsen et al., 2000).

Determining prey suitability is a valuable method for evaluating the biological control potential of a predator species in terms of how its populations can numerically respond to the prey species. For example, if a target pest species is less suitable than other coexisting prey species it is likely that the predator will not control that target pest (Thompson, 1951). As part of a project to examine the dynamics of natural enemies of cereal aphids in Oklahoma, we undertook this study to compare the suitability of the greenbug and bird cherry-oat aphid as prey for *H. convergens*. The experimental approach used in our study differs from the 'standard' approach commonly used in prey suitability studies in two ways. First, whereas the 'standard' approach is to offer *ad libitum* prey to predators, we included low or limited prey levels that ensured high survival and completion of preimaginal development. Our premise is that using low prey levels eliminates the potential confounding effects of satiation (Giles et al., 2001, 2002). Second, whereas the 'standard' approach is to evaluate only single prey species (Hodek and Honek, 1996), we included mixtures of aphid prey species at varying proportions while still maintaining low overall prey levels. Prey mixtures allowed measurement of potential benefits of diet mixing; a phenomenon that is more common in nature than reflected by most prey suitability studies (Hodek and Honek, 1996; Soares et al., 2004). Therefore, a diet that consists of a mixture of greenbugs and bird cherry-oat aphids is probably more representative of a natural diet for *H. convergens* in a winter wheat agroecosystem. Furthermore, offering ladybeetles prey mixtures while limiting prey quantity eliminated the potential confounding effects of prey preference.

2. Materials and methods

2.1. Source of aphids and ladybeetles

Greenbug and bird cherry-oat aphid colonies were maintained on winter wheat (cultivar TAM-105) in a walk-in environmental growth chamber at 22 °C with a 16:8 (L:D) h photoperiod. Wheat was grown in 15-cm diameter pots covered with plexi-glass or acetate cylinders (33-cm tall) that were vented with nylon mesh fabric (in two locations on the cylinder) for air-flow. When plants were approximately 20-cm tall, pots were infested with greenbugs or bird cherry-oat aphids. Aphids were collected daily from plants as needed for the study. When the plants started to show signs of severe injury (significant necrosis), they were removed from the colonies.

Adult *H. convergens* were collected from north-central Oklahoma alfalfa and wheat fields. We maintained 10 individual mating pairs in half-pint (0.24 l) paper cartons (Neptune Paper Products, Jersey City, NJ) covered with fine mesh. Pairs were provided daily with an unlimited supply of greenbugs and bird cherry-oat aphids, moist cotton, and a supplementary wheat–honey–yeast mixture to stimulate egg production. Egg masses from each mating pair were collected daily and separated into 10 ml glass vials stopped with cotton.

2.2. Feeding studies

All experiments were carried out in a table-top environmental chamber at 22 °C and a photoperiod of 16:8 (L:D) h. First instars (<24 h old) that eclosed from *H. convergens* eggs were placed individually in vials stopped with cotton and randomly assigned to one of seven diet treatments (daily quantities and combinations of aphid prey). The diet treatments were (1) 4 mg bird cherry-oat aphids, (2) a mixture of 3 mg bird cherry-oat aphids and 1 mg greenbugs, (3) a mixture of 2 mg bird cherry-oat aphids and 2 mg greenbugs, (4) a mixture of 1 mg bird cherry-oat aphids and 3 mg greenbugs, (5) 4 mg greenbugs, (6) *ad libitum* bird cherry-oat aphids, and (7) *ad libitum* greenbugs. We determined weights of freshly collected aphids by a digital Sartorium M3P microbalance (resolution: 0.001 mg). Thirty *H. convergens* first instars (experimental units) were started on both treatment 1 and 6 whereas 28 instars were started on treatment 2, 33 instars on treatment 3, 36 instars on treatment 4, 32 instars on treatment 5, and 31 instars on treatment 7. Individual larvae assigned to each treatment were drawn from the 10 mating pairs.

Treatments 1 and 5 were designed to measure relative suitability of bird cherry-oat aphids and greenbugs, respectively, at suboptimal prey levels. Treatments 2, 3, and 4 were designed to measure possible benefits of diet mixing (i.e., mixture of aphid prey species at varying proportions) while limited prey quantities eliminated the confounding effects of prey preference. Treatments 6 and 7 were designed to measure the effect of satiation on the relative suitability of the two aphid species.

The relative suitability of the greenbugs and bird cherry-oat aphids was measured as effects on preimaginal development time, preimaginal survival ratios, adult body weight, adult ventral body area, and sex ratio. Larvae and pupae were examined daily to determine survival, larval and pupal stadia. Adults were weighed within 24 h of eclosing using a digital microbalance. Adult body length and width were measured using an ocular micrometer fitted on a zoom stereomicroscope and sex was determined. Adult body length and width were used to calculate the ventral body area, a measure that reflects the body size, using a formula for an ellipse area [$\pi \times 1/2$ (body length) $\times 1/2$ (body width)]. Voucher specimen of *H. convergens*, greenbugs, and bird cherry-oat aphids were deposited in the Department of Entomology and Plant Pathology Museum at Oklahoma State University, Stillwater.

2.3. Statistical analyses

All analyses were performed using SAS version 8.2 for Windows (SAS Institute, 1999). A significance level of 0.05 was chosen for all statistical tests, but sequential Bonferroni adjustments of critical values were used to maintain the Type I error rates at the stated values when multiple tests of a single hypothesis were made (Rice, 1989). We used Fisher's Exact Test (PROC FREQ) to examine the effects of diet treatments on larval and pupal survivorship as well as sex ratios of the individuals that successfully developed to adulthood.

The effects of diet treatments, in conjunction with gender, on preimaginal development and body size of *H. convergens* were assessed by fitting linear mixed models separately for first, second, third, and fourth instars, total larval development, pupal stadium, total immature development time (from hatching to adult eclosion), adult weight (mg), and adult ventral body area (mm^2). Diet treatment, gender, and their interaction were included in the models as fixed effects. Mating pairs were incorporated as random effects. We included mating pair (a surrogate for genotype) as a class variable in these analyses to account for effects of innate (genetic) variation among our sampling units (i.e., individual *H. convergens* larvae). Analysis computations were performed by PROC MIXED using the restricted maximum-likelihood estimation method. When significant interaction between main effects (diet and gender) occurred, the SLICE option in the LSMEANS statement was used to assess the statistical significance of a given factor at different treatment levels of the other factor (i.e., simple effects of diet treatments for each gender) (Schabenberger et al., 2000). If the slice test for a given factor was significant, treatment means (least-squares means) were compared with the DIFF option. We used CONTRAST statements to examine the following preplanned hypotheses: (a) Mean development times for larvae fed limited aphids (i.e., treatments 1 to 5) are no different from mean development times for larvae fed *ad libitum* aphids (i.e., treatments 6 and 7). (b) Mean development times for larvae fed *ad libitum* bird cherry-oat aphids (treatment 6) are no different from those of larvae fed *ad libitum* greenbugs (treatment 7). (c) Mean development times for larvae fed limited bird cherry-oat aphids (treatments 1 and 2) are no different from those of larvae fed limited greenbugs (treatments 4 and 5).

3. Results

3.1. Survival and sex ratios

The overall survival was high in all the diet treatments. The ratios of larvae surviving to pupation did not differ significantly among the diet treatments (Table 1). There was no mortality among the first instars across all treatments whereas three second, four third and four fourth instars died. There were no differences in the proportions of pupae surviving to adulthood (Table 1). All but one pupa survived to adulthood. Preimaginal (combined larval and pupal) survival ratios also did not differ significantly (Table 1).

The proportions of larvae and pupae that developed to become female adults did not differ significantly among the diet treatments (Table 1). Also, when these proportions were individually tested for conforming to the 50:50 sex ratio none of them deviated significantly from that ratio ($P > 0.05$ in all cases).

3.2. Development time

The effect of diet treatment on the development time of *H. convergens* was statistically significant only for the fourth instars; and this likely contributed to significant diet treatment effects for total larval development time as well as total immature development time (from egg hatch

Table 1
Percent of *Hippodamia convergens* surviving through the larval, pupal, and total preimaginal stages when reared on single versus mixed and limited versus *ad libitum* prey of *Rhopalosiphum padi* and *Schizaphis graminum*

Stage	Aphid diet[a]							
	0g4b	1g3b	2g2b	3g1b	4g0b	Ub	Ug	*P*-value[b]
n	30	28	33	36	32	30	31	
Larva	96.7	92.9	90.9	91.7	100	100	93.6	0.385
Pupa	100	100	100	100	100	100	96.6	0.402
Preimaginal	96.7	92.9	90.9	91.7	100	100	90.3	0.220
% Female	57.1	65.4	37.9	43.8	51.6	60.7	67.9	0.206

[a] 0g4b, 4 mg *R. padi*; 1g3b, 1 mg *S. graminum* and 3 mg *R. padi*; 2g2b, 2 mg *S. graminum* and 2 mg *R. padi*; 3g1b, 3 mg *S. graminum* and 1 mg *R. padi*; 4g0b, 4 mg *S. graminum*; Ub, unlimited *R. padi*; Ug, unlimited *S. graminum*.

[b] Fisher's exact test.

to adult eclosion) (Table 2). Fourth instars fed *ad libitum* aphids (treatments 6 and 7) developed faster than those fed limited aphids (treatments 1 to 5) (Contrast test, $F_{1,179} = 24.99$; $P < 0.0001$) (Table 3). The test of Contrast also indicated that the rates of development for fourth instars fed limited bird cherry-oat aphids (treatments 1 and 2) were slower than the rates of development of fourth instars fed limited greenbugs ($F_{1,179} = 4.44$; $P = 0.036$) (Table 3). The development time was 6.2 d for fourth instars on treatment 1, 5.8 d for fourth instars on treatment 2, 5.6 d for treatment 3, 5.3 d for treatment 4, and 5.7 d for treatment 5 (Table 3). Differences between development times of fourth instars on *ad libitum* bird cherry-oat aphids and those of fourth instars on *ad libitum* greenbugs were not significant (Contrast test, $F_{1,179} = 0.00$; $P = 0.974$) (Table 3). Development times of females were significantly longer than those of males during the second and fourth stadia, whereas the opposite was true during the third stadium (Tables 2 and 3). Gender differences in development time during the second and fourth stadia likely contributed to the significant gender effects for total larval and total immature development times (Tables 2 and 3). Lack of significant interaction between diet treatment and gender for development times in Table 2 implies that the effect of either of these factors on *H. convergens* development time did not depend on the level of the other factor.

3.3. Adult body size

Because both the ventral body area and weight of *H. convergens* adults were strongly correlated ($r = 0.879$, $P < 0.0001$) and the analysis of data on body weight gave similar results to those of area we only report on weight as a measure of body size. The weight of *H. convergens* adults differed significantly among the diet treatments and between genders (Table 2). Since the interaction effects between diet and gender were also significant we compared diet treatment means separately for each gender (simple effects) by using the SLICE option of the LSMEANS statement in the MIXED procedure. For both males and females, adult weight was significantly different among diets ($F_{6,\ 179} = 13.02$, $P < 0.0001$ and $F_{6,179} = 37.80$; $P < 0.0001$, respectively). The significant effect of diet on adult weight of both males and females was mostly due to the *ad libitum* aphid diet (Fig. 1). Pairwise comparison of diet treatment means by the DIFF option of the LSMEANS statement showed no significant differences among adult weights of male larvae fed limited aphids (treatments 1 to 5) ($P > 0.05$ in all cases) and no differences

Table 2
The results of analysis of variance (SAS mixed procedure) for development times and adult body size of *H. convergens* reared on single versus mixed and limited versus *ad libitum* prey of *Rhopalosiphum padi* and *Schizaphis graminum*

Response variable	Source of variation	*df*[a]	*F*-value	*P*
1st instar development time	Prey	6, 179	1.39	0.220
	Sex	1, 179	0.03	0.871
	Sex-Prey	6, 179	0.61	0.718
2nd instar development time	Prey	6, 179	1.28	0.271
	Sex	1, 179	9.17	0.003
	Sex-Prey	6, 179	0.42	0.867
3rd instar development time	Prey	6, 179	1.95	0.075
	Sex	1, 179	4.95	0.027
	Sex-Prey	6, 179	1.02	0.413
4th instar development time	Prey	6, 179	5.69	<0.0001
	Sex	1, 179	7.14	0.009
	Sex-Prey	6, 179	0.42	0.863
Total larval development time	Prey	6, 179	3.43	0.003
	Sex	1, 179	7.44	0.007
	Sex-Prey	6, 179	0.38	0.890
Pupal development time	Prey	6, 179	0.57	0.756
	Sex	1, 179	0.27	0.605
	Sex-Prey	6, 179	0.28	0.945
Total immature development time	Prey	6, 179	3.73	0.002
	Sex	1, 179	5.18	0.024
	Sex-Prey	6, 179	0.72	0.631
Adult weight	Prey	6, 54	41.92	<0.0001
	Sex	1,125	9.49	0.002
	Sex-Prey	6, 125	2.49	0.025
Adult ventral area	Prey	6, 54	29.80	<0.0001
	Sex	1,125	23.87	<0.0001
	Sex-Prey	6, 125	2.41	0.029

[a] Analyzed development times are for individuals that survived to the adult stage.

Table 3
Duration in days of developmental stages of *Hippodamia convergens* reared on varying prey quantities and mixtures of *Rhopalosiphum padi* and *Schizaphis graminum* at 22 °C and photoperiod of 16:8 (L:D) h (mean ± SE)

Stage	Aphid diet[a]						
Sex	0g4b	1g3b	2g2b	3g1b	4g0b	Ug	Ub
1st instar							
Female	3.4 ± 0.3Aa	3.2 ± 0.3Aa	3.2 ± 0.3Aa	3.0 ± 0.3Aa	2.8 ± 0.3Aa	3.1 ± 0.3Aa	3.0 ± 0.3Aa
Male	3.1 ± 0.3Aa	3.0 ± 0.4Aa	3.5 ± 0.3Aa	3.0 ± 0.3Aa	2.9 ± 0.3Aa	3.5 ± 0.4Aa	2.8 ± 0.3Aa
2nd instar							
Female	2.5 ± 0.2Aa	2.5 ± 0.2Aa	2.8 ± 0.2Aa	2.8 ± 0.2Aa	3.0 ± 0.2Aa	2.8 ± 0.2Aa	2.9 ± 0.2Aa
Male	2.3 ± 0.2Aa	2.4 ± 0.3Aa	2.5 ± 0.2Aa	2.6 ± 0.2Aa	2.5 ± 0.2Ba	2.2 ± 0.3Ba	2.6 ± 0.2Aa
3rd instar							
Female	3.2 ± 0.2Aa	3.0 ± 0.2Aa	2.9 ± 0.2Aa	2.7 ± 0.2Aa	2.8 ± 0.2Aa	2.9 ± 0.2Aa	2.9 ± 0.2Aa
Male	3.3 ± 0.2Aa	3.0 ± 0.2Aa	3.0 ± 0.2Aa	2.9 ± 0.2Aa	3.2 ± 0.2Aa	3.0 ± 0.2Aa	3.6 ± 0.2Ba
4th instar							
Female	6.2 ± 0.4Aa	6.2 ± 0.4Aa	5.9 ± 0.4Aa	5.5 ± 0.4Aa	6.0 ± 0.4Aa	4.8 ± 0.4Ab	5.1 ± 0.4Ab
Male	6.1 ± 0.4Aa	5.3 ± 0.5Aa	5.3 ± 0.4Aa	5.1 ± 0.4Aa	5.5 ± 0.4Aa	4.8 ± 0.5Ab	4.5 ± 0.4Ab
Total larval							
Female	15.3 ± 0.6Aa	14.9 ± 0.6Aa	14.8 ± 0.7Aa	14.1 ± 0.7Aa	14.7 ± 0.6Aa	13.6 ± 0.6Ab	13.9 ± 0.6Ab
Male	14.8 ± 0.7Aa	13.6 ± 0.7Aa	14.1 ± 0.6Aa	13.6 ± 0.6Aa	14.0 ± 0.6Aa	13.5 ± 0.7Ab	13.4 ± 0.7Ab
Pupa							
Female	6.7 ± 0.4Aa	6.9 ± 0.4Aa	7.2 ± 0.4Aa	7.0 ± 0.4Aa	7.1 ± 0.4Aa	6.7 ± 0.4Aa	6.7 ± 0.4Aa
Male	7.1 ± 0.4Aa	6.8 ± 0.5Aa	7.0 ± 0.4Aa	7.1 ± 0.4Aa	7.1 ± 0.4Aa	6.8 ± 0.4Aa	7.0 ± 0.4Aa
Total immature							
Female	22.0 ± 0.9Aa	21.9 ± 0.9Aa	22.0 ± 0.9Aa	21.1 ± 0.9Aa	21.8 ± 0.9Aa	20.3 ± 0.9Ab	20.5 ± 0.9Ab
Male	21.9 ± 0.9Aa	20.3 ± 0.9Aa	21.2 ± 0.9Aa	20.6 ± 0.9Aa	21.0 ± 0.9Aa	20.3 ± 0.9Ab	20.5 ± 0.9Ab

For each stage, means followed by the same upper case letter in the same column and by the same lower case letter in the same row are not significantly different at $P = 0.05$.

[a] 0g4b, 4 mg *R. padi*; 1g3b, 1 mg *S. graminum* and 3 mg *R. padi*; 2g2b, 2 mg *S. graminum* and 2 mg *R. padi*; 3g1b, 3 mg *S. graminum* and 1 mg *R. padi*; 4g0b, 4 mg *S. graminum*; Ub, unlimited *R. padi*; Ug, unlimited *S. graminum*.

among female larvae fed limited aphids ($P > 0.05$ in all cases) (Fig. 1). However, for both males and females, the weight of *H. convergens* adults that were fed *ad libitum* aphids as larvae was significantly heavier than that of adults fed limited aphids as larvae ($P < 0.0001$ in all cases) (Fig. 1). The significant diet-by-gender interaction was caused by the weight of adult females fed *ad libitum* greenbugs as larvae being significantly heavier than that of females fed *ad libitum* bird cherry-oat aphids ($P = 0.0002$), whereas no significant difference existed between weights of males ($P = 0.320$) (Fig. 1).

4. Discussion

Our results indicate that bird cherry-oat aphid and greenbugs are similar in nutritive value with regard to preimaginal survival. Similar results have been found in other aphidophagous ladybeetles when fed different species of cereal aphids, including bird cherry-oat aphids (Hauge et al., 1998; Özder and Sağlam, 2003). Lack of significant differences in survival levels among our diet treatments also revealed that the amount of aphids that we considered suboptimal or limited were quite adequate for completing preimaginal development. High survival levels have also been reported for *H. convergens*, *C. septempinctata* and *Coleomegilla maculata* (DeGeer) reared on pea aphids, *Acyrthosiphon pisum* Harris, at amounts similar to our limited diet regimes (Giles et al., 2001; Obrycki et al., 1998).

The influence of diet treatments on *H. convergens* rate of development was seen only among fourth instars in our study. This implies that a diet of 4 mg of aphids per day was not limiting for the first, second, and third instars, and that greenbugs and bird cherry-oat aphids had equivalent nutritive value for these instars as well as for the pupal stage. The effects of diet on the development times of fourth instars were in the form of aphid quantity and quality. Fourth instars that fed on *ad libitum* aphids had shorter development time than those that fed on limited amounts (1 d difference). Lack of significant differences between development times of fourth instars fed *ad libitum* bird cherry-oat aphids and greenbugs and lack of differences among all diet treatment groups of first, second, and third instars point to the potential of satiation in masking diet effects on development time. Manifestation of differences in nutritive value in terms of prey quantity only among the fourth instars is not unexpected as this is the stage that consumes a lot more food than the younger (1st to 3rd) instars (Hodek and Honek, 1996). For example, fourth instars of another ladybeetle, *Semiadalia undecimnotata* Schneider, were found to consume >80% of all the food consumed during the larval stage (Ferran and Larrogue, 1977). The high food consumption by fourth instars is also an indication of the eco-physiological significance of this

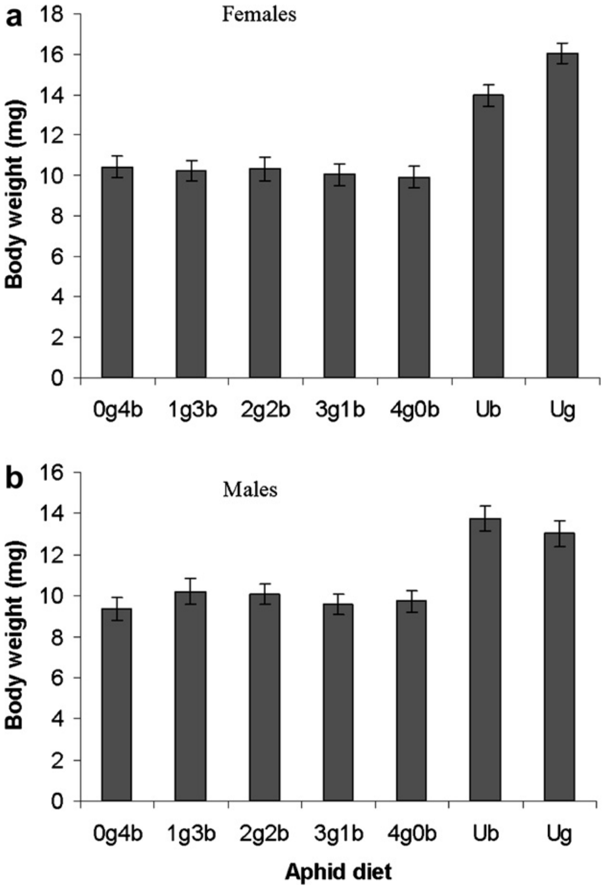

Fig. 1. Fresh body weight (least squares means ± SE) of adult *Hippodamia convergens* reared on single versus mixed and limited versus *ad libitum* prey of *Rhopalosiphum padi* and *Schizaphis graminum* at 22 °C and a photoperiod of 16:8 (L:D) h. 0g4b, 4 mg *R. padi*; 1g3b, 1 mg *S. graminum* and 3 mg *R. padi*; 2g2b, 2 mg *S. graminum* and 2 mg *R. padi*; 3g1b, 3 mg *S. graminum* and 1 mg *R. padi*; 4g0b, 4 mg *S. graminum*; Ub, unlimited *R. padi*; Ug, unlimited *S. graminum*. Female sample sizes are: 0g4b, 16; 1g3b, 17; 2g2b, 11; 3g1b, 14; 4g0b, 16; Ub, 17; Ug, 19. Male sample sizes are: 0g4b, 12; 1g3b, 9; 2g2b, 18; 3g1b, 18; 4g0b, 15; Ub, 11; Ug, 9.

developmental stage in ladybeetles since the final size attained during this stage determines adult size.

Differences in the nutritive quality between bird cherry-oat aphids and greenbugs were evident only when the comparison was among the limited aphid amounts. This observed difference in nutritive value (in terms of prey quality) among the fourth instars is in line with observations in other ladybeetle species (Hodek and Honek, 1996; Özder and Sağlam, 2003). For example, Smith (1965) and Obrycki and Orr (1990) found that differences in preimaginal development of several ladybeetle species fed pea aphids, *A. pisum*, and corn leaf aphids, *Rhopalosiphum maidis* (Fitch), were mainly due to the longer fourth stadia for the larvae given food of lower quality (i.e., *R. maidis*). It is important to note that the above-mentioned studies obtained significant effects of prey quality under *ad libitum* food conditions whereas in our study we could only observe such effects under limited food conditions, thus suggesting satiation as a potential confounding factor.

Diet treatments had different effects on *H. convergens* body size (weight and ventral body area) compared to effects on development time and survival. The significant effects on body size were a result of larvae feeding on *ad libitum* aphids of both species developing into much heavier and larger adults than for the larvae that fed on limited aphids. The difference in body size of ladybeetles as a consequence of feeding on different prey quantities or qualities has been well documented (Dixon, 2000; Hodek and Honek, 1996). Our study also showed that for the larvae fed *ad libitum* aphids, the effects of gender and diet-by-gender interaction were significant on body size.

Body size for females in many insect species appears to be more sensitive to environmental conditions than male body size (Teder and Tammaru, 2005). This may be the basis for the interaction between diet and gender on body size seen in our study. Bird cherry-oat aphids were of lower nutritive quality than greenbugs only for females under *ad libitum* food conditions. What this suggests is that, for *H. convergens*, diet (quality) effects on body size are not significant at suboptimal food amounts because nutrient supply is just enough to allow fourth instars to grow to the threshold size beyond which pupation is possible. Threshold sizes for pupation and metamorphosis are common in many insects (Nijhout, 1981; de Moed et al., 1999) and we assume that ladybeetles are no exception. Furthermore, threshold sizes are invariant for each species and are associated with latent periods during which, if food is available, further growth occurs (Nijhout and Williams, 1974).

The hypothesis that we propose regarding *H. convergens* is that soon after reaching the critical size, the fourth instars that were fed limited aphids (treatments 1 to 5) underwent metamorphosis into the pupal stage (i.e., relatively shorter latent periods) as a result of the suboptimal prey quantity. The fourth instars that were given *ad libitum* aphids (treatment 6 and 7) continued to feed and grow beyond the threshold size (i.e., relatively longer latent periods) because of food abundance. However, the rate of growth during the latent period was faster for female larvae on greenbugs than on bird cherry-oat aphids, whereas male larval growth rates were not different between the two aphid species, thus reflecting higher sensitivity to prey quality by females (Teder and Tammaru, 2005). The lack of significant difference in preimaginal survival levels among all the treatments also supports the idea of a threshold size for pupation because if the amount of food is just enough to allow growth and development to this threshold size then all individual larvae should potentially survive to become adults in spite of differences in body size. This may be an evidence of *H. convergens* adaptation for coping with frequent food shortages in field conditions.

As shown by our study, the relative suitability of greenbugs is higher than that of bird cherry-oat aphids although this does not apply to all the life history traits of *H. convergens*. Similar results showing inferior nutritional position of bird cherry-oat aphids to ladybeetles relative to other cereal aphids have been reported (Hauge et al., 1998; Özder and Sağlam, 2003). Reasons for the inferior nutritional value of bird cherry-oat aphids are not clear as the aphids had the common host plant. Our results also provide evidence that prey suitability studies that only use *ad libitum* food amounts do not adequately assess effects of prey quality as some of these can be masked by satiation. We also argue that using only *ad libitum* amounts, which predators do not normally experience in the field, has the same shortcoming as conducting studies with prey species that may not be encountered by the predator in nature (Majerus, 1994; Hodek and Honek, 1996). In terms of biological control, it would seem that in situations where greenbug populations are isolated from those of bird cherry-oat aphid *H. convergens* would have a better potential of controlling outbreaks of the former aphid species. But in areas where they co-occur there should not be significant differences unless there is prey preference involved.

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