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Dietary complementation across life stages in the polyphagous lady beetle  
*Coleomegilla maculata*

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### How to cite this manuscript

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Michaud, J.P., & Jyoti, J.L. (2008). Dietary complementation across life stages in the polyphagous lady beetle *Coleomegilla maculata*. Retrieved from <http://krex.ksu.edu>

### Published Version Information

**Citation:** Michaud, J.P., & Jyoti, J.L. (2008). Dietary complementation across life stages in the polyphagous lady beetle *Coleomegilla maculata*. *Entomologia Experimentalis et Applicata*, 126(1), 40-45.

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**Digital Object Identifier (DOI):** doi: 10.1111/j.1570-7458.2007.00636.x

**Publisher's Link:** <http://www.wiley.com/bw/journal.asp?ref=0013-8703>

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1 Running head:

2 Michaud & Jyoti, Dietary complementation in *Coleomegilla maculata*

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7 **Dietary complementation across life stages in the polyphagous**  
8 **lady beetle *Coleomegilla maculata***

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20 *Key words:* Coccinellidae, Coleoptera, development, *Ephestia kuehniella*, fitness, pollen,

21 reproduction, *Schizaphis graminum*, generalist predator

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25 Accepted: 3 September 2007

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29 **Abstract**

30

31 We investigated the life history consequences of changes in diet between larval and adult  
32 life stages in the polyphagous lady beetle *Coleomegilla maculata* DeGeer (Coleoptera:  
33 Coccinellidae). Beetles were reared on three larval diets: greenbug, *Schizaphis*  
34 *graminum* Rondani (Homoptera: Aphididae), eggs of the flour moth, *Ephestia kuehniella*  
35 Zeller (Lepidoptera: Pyralidae), and bee pollen. The reproductive performance of  
36 females was then evaluated on an adult diet of either greenbug or moth eggs. Moth eggs  
37 appeared to be the most suitable diet for larvae, yielding the largest adults, and pollen the  
38 least suitable, resulting in the smallest adults and greatly extended developmental time.  
39 Pollen-reared beetles tended to have lower fecundity and fertility than those reared on  
40 animal protein, regardless of adult diet. Female fitness was generally increased by a  
41 change in diet upon emergence to the alternative source of animal protein, suggesting that  
42 dietary complementation occurred across life stages. Among females reared on  
43 greenbug, a change of diet to moth eggs reduced the period required for production of 12  
44 clutches and increased egg fertility compared to continued feeding on greenbug. Among  
45 females reared on moth eggs, a change of diet to greenbug increased fecundity compared  
46 to continued feeding on moth eggs. Among females fed an adult diet of greenbug, those  
47 fed moth eggs as larvae had faster production of 12 clutches and higher fecundity. We  
48 discuss these novel results in the context of coccinellid life history and ecology and their  
49 potential implications for other insects that are predatory as both larvae and adults.

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## 60 **Introduction**

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62 Holometabolous insects have a complex life history consisting of four distinct life stages,  
63 each with highly specific functions. The sole function of the egg and pupal stages is  
64 cellular differentiation: these neither feed nor grow but simply develop. Although adult  
65 insects may feed, they neither grow nor develop, but are specialized for reproduction. In  
66 contrast, larvae comprise the only life stage responsible for growth and, in some insects,  
67 is the only stage that feeds. Thus, the size of adult insects is typically determined by the  
68 quantity and quality of the larval diet, within genetic constraints (e.g., Conner et al.,  
69 1989, Moczek, 1998). Adult body size has the potential to influence fitness through  
70 effects on survival, mating success, or fecundity (Hone & Benton, 2005; Blanckenhorn,  
71 2005; Cratsley & Lewis, 2005; Himuro et al., 2006; Kemp et al., 2006). Thus, the larval  
72 diet may influence adult fitness through direct effects on body size, or via ‘larval  
73 legacies’, chemical residues that may influence mating success (Conner et al., 1989) or  
74 behavioral responses to environmental stimuli (Corbet, 1985; Anderson et al., 1995;  
75 Gandolfi et al., 2003; Raylor & Munson, 2004).

76 Although herbivorous insects tend to demonstrate strong consistencies between  
77 larval and adult food plants, insects that are predaceous as both larva and adult may not  
78 necessarily feed on the same prey in both life stages. For example, Murdoch (1969)  
79 demonstrated that foraging predators may switch among prey types to concentrate on  
80 those that are most abundant. However, surprisingly few studies have addressed the  
81 possible consequences of mixed diets or prey switching in predatory insects. Soares et al.  
82 (2004) examined effects of mixed diets on the adult performance of *Harmonia axyridis*  
83 Pallas but did not test for effects across life stages. Hauge et al. (1998) found that  
84 *Coccinella septempunctata* L. raised on a mixed diet of three aphid species were  
85 intermediate in developmental time and adult weight to individuals raised on single aphid  
86 species that varied in suitability as prey, but they did not evaluate adult reproductive  
87 performance. Hattingh & Samways (1992) found that a change in prey during the larval  
88 stage had adverse consequences for the development of two *Chilocorus* spp., and that a  
89 change in adult diet caused temporary reductions in female reproductive performance, but  
90 they did not test for interactions between larval and adult diets. Other studies have tested

91 the effects of mixed versus monotypic diets in generalist predators such as carabid beetles  
92 (Jorgensen & Toft, 1997; Toft, 2005; Fawki & Toft, 2005) and spiders (Oelbermann &  
93 Scheu, 2002; Allard & Yeargan, 2005) with somewhat mixed results.

94 The twelve-spotted lady beetle, *Coleomegilla maculata* DeGeer (Coleoptera:  
95 Coccinellidae), is a relatively polyphagous coccinellid species and, consequently, one of  
96 the easiest to rear on factitious diets (Hodek & Honěk, 1996). Unlike other primarily  
97 aphidophagous species, *C. maculata* can complete development on a diet of pollen  
98 without any source of animal protein, although the period of development is substantially  
99 increased and adult size reduced (Lundgren & Weidenmann, 2004; Michaud & Grant,  
100 2005). It is also known to feed regularly on the eggs of various Lepidoptera (Phoofolo et  
101 al., 2001; Pfannenstiel & Yeargen 2002; Musser & Shelton, 2003). The polyphagous  
102 habits of this species render it eminently well suited for exploration of larval-adult diet  
103 interactions because viable adults can be reared on larval diets that vary greatly in  
104 suitability.

105 In the present study, we reared *C. maculata* on three larval diets and then  
106 examined the reproductive performance of the resulting adult females on two adult diets  
107 known to support successful reproduction. Two possible effects were hypothesized, one  
108 positive and one negative. If females demonstrated superior reproductive performance  
109 after a change in diet between life stages compared to those receiving the same diets as  
110 both larva and adult, dietary complementation across life stages would be indicated. On  
111 the other hand, if females receiving a change of diet demonstrated inferior reproductive  
112 performance compared to those receiving monotypic diets as both adult and larva, an  
113 interference effect of the change in diet would be indicated.

114

## 115 **Materials and methods**

116

### 117 **Insect colony**

118 A colony of *C. maculata* was established from adult beetles collected from maize plants  
119 in Hays, KS, USA in early May, 2006. All insect life stages were held in a growth  
120 chamber with L16:D8 day length at a temperature of  $24 \pm 1$  °C. Adult females were  
121 isolated in plastic Petri dishes (5.5 cm in diameter) and fed a diet of frozen eggs of the

122 flour moth, *Epehstia kuehniella* Zeller (Lepidoptera: Pyralidae) (Beneficial Insectary,  
123 14751 Oak Run Road, Oak Run, CA, USA) with water provided on a small cube of  
124 sponge, both refreshed every 2nd day. All insects used in experiments were only one  
125 generation removed from field-collected adults. Egg clusters, typically laid on inner  
126 surfaces of the Petri dishes, were collected daily by transferring the beetles to new dishes,  
127 or simply switching the lids. Egg clusters were held for 4 days until eclosion of larvae.  
128 Larvae of the first laboratory generation were reared on frozen eggs of *E. kuehniella* and  
129 offspring of the resulting adults were used in the experiment.

130

### 131 **Experimental design**

132 The experiment consisted of a factorial arrangement of three larval diets × two adult diets  
133 in a completely randomized design and was conducted under same physical conditions  
134 used for rearing the beetle colony. Eighty neonate larvae were isolated in Petri dishes  
135 upon eclosion and then reared through to the adult stage on each of three diets: 1) eggs of  
136 *E. kuehniella* + water, 2) greenbugs, *Schizaphis graminum* Rondani (Homoptera:  
137 Aphididae), and 3) pulverized bee pollen + water. We ensured that each clutch of  
138 neonates was equally divided among treatments. All insects were examined daily  
139 throughout the experiment and developmental time was tallied as the number of days  
140 from eclosion of the egg to formation of a pre-pupa. Callow adults were weighed on an  
141 analytical balance within a few hours of emergence and then isolated in Petri dishes.  
142 Insects from each of the three larval diets were then subdivided into two adult diets,  
143 either eggs of *E. kuehniella* or greenbug. Pollen was not employed as an adult diet  
144 because it does not support reproduction. Groups of adults emerging from the same  
145 treatments were brought together after they were 5-7 days old so that mating pairs could  
146 be established. These pairs were then held together in Petri dishes for the duration of the  
147 experiment.

148

### 149 **Data collection**

150 As females became reproductive, we collected and counted their egg clusters daily and  
151 recorded the number of eggs that subsequently hatched until we had collected a total of  
152 12 days of reproduction from each female. As the bulk of female reproductive effort

153 occurs during the first weeks of reproductive life (Dixon & Agarwala, 2002), it is not  
154 necessary to collect lifetime fecundity in order to evaluate effects of diet on reproductive  
155 performance (Michaud, 2005; Michaud & Grant, 2005). We calculated the  
156 prereproductive period of each female as the number of days from adult emergence until  
157 production of her first egg cluster, and the reproductive period as the number of days  
158 required to achieve 12 days of oviposition. Fecundity was tallied as the total number of  
159 eggs laid in 12 days of reproduction. Fertility was estimated in two ways; by the  
160 percentage of eggs that hatched for each female, and by the number of larvae produced  
161 per female.

162

### 163 **Statistical analysis**

164 Data for developmental time and adult fresh weight upon emergence were analyzed in a  
165 completely randomized design, whereas reproductive performance data were analyzed in  
166 a  $3 \times 2$  factorial arrangement in a completely randomized design with PROC GLM. (SAS  
167 Institute, 2003). Treatment means were separated by multiple t-tests obtained from the  
168 least square means statement and significance levels adjusted using Bonferroni's  
169 correction for multiple comparisons ( $\alpha = 0.05$ ). Linear regression was used to test the  
170 relationship between developmental time and adult emergence weight.

171

## 172 **Results**

173

### 174 **Development**

175 The percentage of larvae pupating successfully in the three treatments was 96.3, 91.6, and  
176 49.4% on the greenbug, flour moth, and pollen diets, respectively. A test of proportions  
177 (StatSoft, 2000) revealed that survival to pupation on the pollen diet was significantly  
178 lower than on either the greenbug or flour moth diets ( $P < 0.001$  in both cases). An  
179 additional eight individuals on the pollen diet died as pupae, reducing survivorship to  
180 39.0 % on this diet. Mean developmental times and fresh weights of callow adults are  
181 given in Figures 1 and 2, respectively. Considering all insects that pupated successfully,  
182 developmental time was significantly and negatively correlated with fresh adult weight ( $F$   
183  $= 200.17$ , d.f. = 183,  $P < 0.001$ ,  $r^2 = 0.522$ ).

184

**185 Reproduction**

186 We obtained a total of 12 days of reproduction from 15 females in the greenbug-greenbug  
187 treatment, 17 females in the greenbug-flour moth treatment, nine females in the flour  
188 moth-greenbug treatment, 19 females in the flour moth-flour moth treatment, six females  
189 in the pollen-greenbug treatment, and six females in the pollen-flour moth treatment.

190 Data for reproductive period, fecundity, and fertility are reported in Table 1. The  
191 prereproductive period averaged  $14.8 \pm 1.1$  days and did not vary significantly as a  
192 function of diet. When greenbug was the larval diet, adult females required fewer days to  
193 produce 12 clutches and had significantly higher fertility (both measures) when fed moth  
194 eggs than when fed greenbug, but did not differ in fecundity. When moth eggs were the  
195 larval diet, adult females fed greenbug had higher fecundity than those fed moth eggs,  
196 whereas other measures of performance did not differ between adult diets. When pollen  
197 was the larval diet, adult females did not differ in any measure of performance between  
198 adult diets.

199 When the adult diet was greenbug, the larval diet of moth eggs resulted in higher  
200 fecundity and fertility than either greenbug or pollen (Table 1). When moth eggs were  
201 the adult diet, adult females reared on pollen had lower fecundity and fertility than those  
202 reared on greenbug or moth eggs, and females reared on greenbug produced 12 clutches  
203 in a shorter period than those fed moth eggs or pollen.

204

**205 Discussion**

206

207 Michaud (2005) argued that prey suitability may differ for larval and adult  
208 coccinellids and should be evaluated separately. Adult coccinellids have stronger  
209 mandibles and more highly developed digestive systems than do larvae and likely process  
210 some types of food more efficiently. For example, coccinellid larvae typically suck the  
211 body contents of aphids leaving an empty shell, whereas adults consume whole aphids,  
212 including the cuticle, such that a careful examination of gut contents can be used to  
213 identify prey types (Mendel et al., 1985). Furthermore, larvae utilize resources for  
214 growth and development, whereas adults use them for dispersal and reproduction, and the



215 nutritional demands of these various functions may differ. The present findings underline  
216 the importance of assessing prey suitability separately for adults and larvae when species  
217 are predatory in both life stages, and the importance of considering possible interactions  
218 between larval and adult diets.

219 In our experiment, the highest fecundity and fertility were obtained when female  
220 *C. maculata* were reared on moth eggs and then switched to a diet of greenbugs as adults.  
221 Females reared on greenbug and switched to moth eggs upon emergence had higher  
222 fertility than females that remained on greenbugs and the latter required 10 extra days to  
223 produce a quota of 12 clutches. One explanation for these results is that both diets are  
224 nutritionally limiting to some degree, despite being 'essential foods' as originally defined  
225 by Hodek & Honěk (1996), and 'adequate diets' for both life stages as defined by  
226 Michaud (2005). Thus, certain nutrients acquired by larvae remained available to  
227 complement deficiencies in the adult diet that otherwise limited female fitness. To our  
228 knowledge, this is a novel result that we refer to as dietary complementation across life  
229 stages.

230 Results of feeding studies with another coccinellid, *Cycloneda sanguinea* L., also  
231 revealed nutritional legacies of larval diets for female reproductive performance  
232 (Michaud, 2000). Females had higher fertility on an adult diet of *Aphis spiraecola* Patch  
233 compared to *Toxoptera citricida* (Kirkaldy), a prey that seemed to impair egg fertility  
234 even though it supported high fecundity. However, when larvae were raised on a diet  
235 alternating daily between the two aphid species, and then fed only one prey type as  
236 adults, the fertility of females on the *T. citricida* diet declined significantly after 1 week  
237 as the nutritional legacy of *A. spiraecola* from the larval diet became exhausted.  
238 Meanwhile, the fertility of females on the *A. spiraecola* diet began to increase after a  
239 similar period as the negative influence of *T. citricida* from the larval diet decayed.  
240 There was no indication of decay in the effects observed in the present study, but it seems  
241 likely that some forms of nutritional complementation across life stages may be more or  
242 less permanent than others.

243 Larvae of *C. maculata* fed exclusively pollen experienced delayed development  
244 and substantially reduced adult weight (Figure 1), consistent with previous observations  
245 of this species (Lundgren & Weidenmann, 2004; Michaud & Grant, 2005). The negative

246 relationship between developmental time and adult weight in coccinellids is well  
247 recognized (Dixon, 2000). Similarly, Tarango & Quiñones (2001) showed that  
248 developmental time of *Harmonia axyridis* Pallas was lengthened as daily food rations  
249 were reduced. Thus, protracted periods of development in coccinellids may compensate  
250 for either reduced food quantity or reduced food quality. Dixon (2000) reasoned that  
251 aphidophagous lady beetles develop as fast as is possible for such insects, and in parallel  
252 with the fast development of their aphid prey. Aphid colonies represent highly ephemeral  
253 resources that can be very abundant, but only for short periods. Under these conditions,  
254 rapid development of larvae is advantageous and selection may favor mechanisms that  
255 couple increases in developmental rate with increases in growth rate such that fast  
256 development does not exact a cost in terms of adult body size.

257         Previously, Michaud & Grant (2005) found that maize pollen, sorghum pollen,  
258 and pulverized bee pollen, all supported successful development in *C. maculata* with  
259 survival to adulthood that did not differ significantly from 100%, provided water was  
260 made available. The relatively low survival of larvae on the pollen diet in this study was  
261 unexpected and was likely a function of the pollen source ('organic' powdered bee pollen  
262 obtained from an online retailer) being somewhat stale. However, pollen was specifically  
263 selected to serve as an inferior larval diet and survival was sufficient to permit evaluation  
264 of adult performance.

265         Notably, females reared on pollen did not differ dramatically in reproductive  
266 performance from those fed on animal prey and were not significantly less fecund or less  
267 fertile compared to females fed a continuous diet of greenbug. It is conceivable that the  
268 female reproductive system is not irreversibly compromised by a marginal larval diet,  
269 provided that a more adequate diet is obtained shortly after emergence. It is also possible  
270 that the smaller pollen-fed females produced proportionally smaller eggs such that their  
271 number was not substantially reduced, an effect that could have gone unnoticed in the  
272 experiment.

273         Legacies of larval experience on adult behavior such as those observed in aphid  
274 parasitoids (Wickremasinghe & van Emden, 1992; Storeck et al., 2000; Douloumpaka &  
275 van Emden, 2003) typically guide adults to the same plants that harbored the larval host,  
276 and presumably the same host species. Possible legacy effects of larval prey plants have

277 not yet been tested in coccinellids but we suspect that such mechanisms are adaptive only  
278 for species that are relatively short-lived, develop quickly, and have limited dispersal  
279 ability. Such insects are more likely to benefit from host- or prey-plant fidelity than are  
280 longer-lived, more polyphagous species that frequently experience changes in prey  
281 availability within the time frame of a single generation.

282 Coccinellid populations in temperate regions frequently undergo seasonal shifts  
283 among prey habitats. Reproductive diapause and migration are common features of  
284 aphidophagous coccinellids and both facilitate eurytopy, broad dispersal, and the  
285 sequential exploitation of different prey species. Consequently, dietary complementation  
286 could emerge as an important factor affecting the fitness of migrant coccinellids that  
287 change habitats as pre-reproductive adults. It might be worthwhile to test for similar  
288 effects in other beneficial insects that are predatory as both larvae and adults since dietary  
289 complementation could have useful applications in augmentation programs.

290

## 291 **Acknowledgements**

292

293 The authors thank Phil Sloderbeck for constructive comments on the manuscript.  
294 Voucher specimens of *C. maculata* are deposited at the Prairie Museum of Arthropod  
295 Research in Manhattan, KS under reference number 192. This publication is contribution  
296 No. 07-311-J of the Kansas State Agricultural Experiment Station.

297

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393 of their aphid prey. *Physiological Entomology* 17: 297-304.
- 394

394 **Table 1.** Mean ( $\pm$  SEM) values for the reproductive performance of female *Coleomegilla*  
 395 *maculata* revealing interactions between larval and adult diets. Larvae were fed one of  
 396 three diets and the adults obtained in each treatment further subdivided into two groups,  
 397 each fed one of two adult diets  
 398

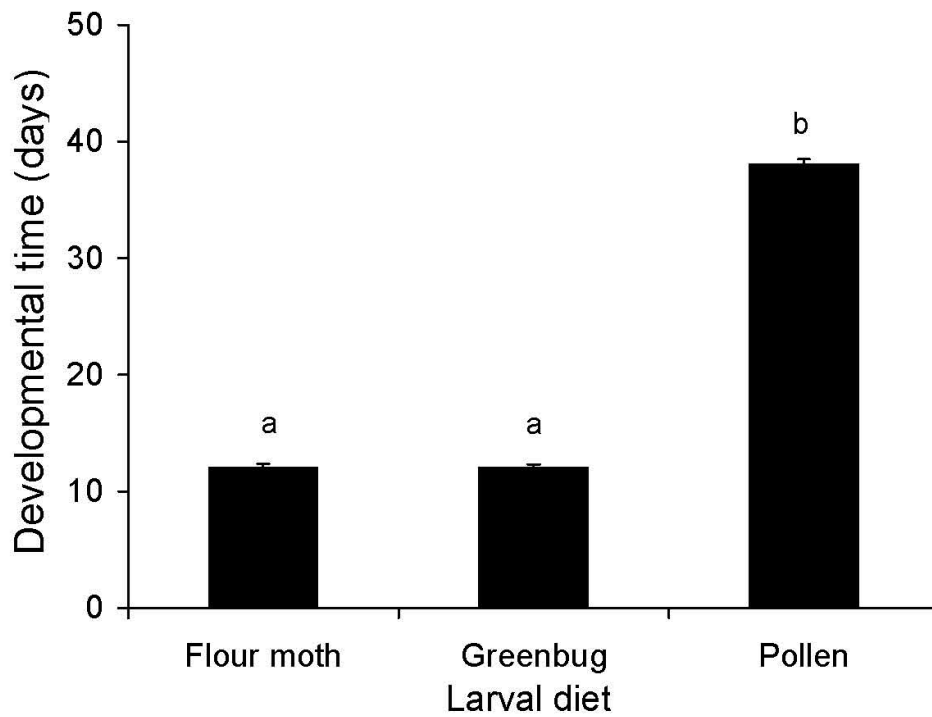
Larval diet	Adult diet	
	Greenbug	Flour moth
Pre-reproductive period (days)		
Greenbug	14.9 $\pm$ 2.5aA	14.9 $\pm$ 2.3aA
Flour moth	10.9 $\pm$ 3.2aA	16.4 $\pm$ 2.2aA
Pollen	15.8 $\pm$ 3.9aA	14.3 $\pm$ 3.9aA
$F_{2,66} = 0.76, P = 0.4705$		
Reproductive period (days)		
Greenbug	30.1 $\pm$ 2.5aA	20.1 $\pm$ 2.3bB
Flour moth	22.2 $\pm$ 3.2bA	23.1 $\pm$ 2.2aA
Pollen	28.5 $\pm$ 3.9aA	23.7 $\pm$ 3.9aA
$F_{2,66} = 2.20, P = 0.1189$		
Fecundity (no. eggs /female)		
Greenbug	138.7 $\pm$ 11.4bA	161.3 $\pm$ 10.7aA
Flour moth	182.4 $\pm$ 14.7aA	146.3 $\pm$ 10.1aB
Pollen	125.8 $\pm$ 17.7bA	106.5 $\pm$ 17.9bA
$F_{2,66} = 3.26, P = 0.0449$		
Fertility (% egg hatch)		
Greenbug	42.4 $\pm$ 4.2bB	65.8 $\pm$ 3.9aA
Flour moth	68.8 $\pm$ 5.4aA	68.1 $\pm$ 3.7aA
Pollen	49.1 $\pm$ 6.6bA	46.7 $\pm$ 6.6bA
$F_{2,66} = 5.13, P = 0.0085$		
Fertility (no. larvae/female)		
Greenbug	58.0 $\pm$ 10.8bB	108.1 $\pm$ 10.2aA
Flour moth	129.4 $\pm$ 13.9aA	101.1 $\pm$ 9.6aA
Pollen	66.8 $\pm$ 17.1bA	50.3 $\pm$ 17.1bA
$F_{2,66} = 6.78, P = 0.0021$		

399 Means followed by the same lower case letter were not significantly different within  
 400 columns; those followed by the same upper case letter were not significantly different  
 401 within rows ( $\alpha = 0.05$ ). Treatment means were separated by multiple t-tests obtained  
 402 from the least square means statement and significance levels adjusted using Bonferroni's  
 403 correction for multiple comparisons.  
 404

404 **Fig.1.** Mean (+ SEM) developmental times (from eclosion to formation of a prepupa) of  
405 *Coleomegilla maculata* larvae reared on 1) eggs of *Ephestia kuehniella*, 2) greenbug,  
406 *Schizaphis graminum*, and 3) bee pollen. Columns bearing the same letter were not  
407 significantly different ( $\alpha > 0.05$ ).

408

410



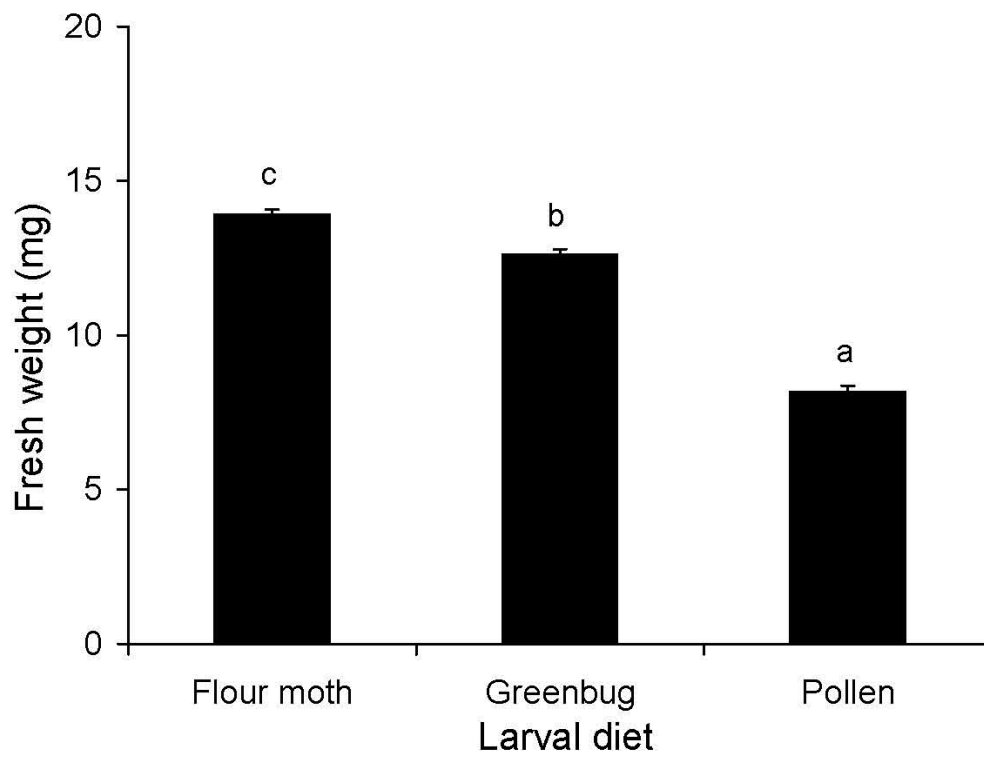


411

412 **Fig.2.** Mean (+ SEM) fresh emergence weights of *Coleomegilla maculata* adults reared  
413 on 1) eggs of *Ephestia kuehniella*, 2) greenbug, *Schizaphis graminum*, and 3) bee pollen.

414 Columns bearing the same letter were not significantly different ( $\alpha > 0.05$ ).

415



416

