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

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7   **Dietary complementation across life stages in the polyphagous**

8   **lady beetle *Coleomegilla maculata***

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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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Introduction

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 ± 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, *Ephestia 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 × 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 ± 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 complimentation could have useful applications in augmentation programs.

290

297

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394

394 **Table 1.** Mean (± 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 ± 2.5aA	14.9 ± 2.3aA
Flour moth	10.9 ± 3.2aA	16.4 ± 2.2aA
Pollen	15.8 ± 3.9aA	14.3 ± 3.9aA
	$F_{2,66} = 0.76$, $P = 0.4705$	
Reproductive period (days)		
Greenbug	30.1 ± 2.5aA	20.1 ± 2.3bB
Flour moth	22.2 ± 3.2bA	23.1 ± 2.2aA
Pollen	28.5 ± 3.9aA	23.7 ± 3.9aA
	$F_{2\,66} = 2.20$, $P = 0.1189$	
Fecundity (no. eggs /female)		
Greenbug	138.7 ± 11.4bA	161.3 ± 10.7aA
Flour moth	182.4 ± 14.7aA	146.3 ± 10.1aB
Pollen	125.8 ± 17.7bA	106.5 ± 17.9bA
	$F_{2,66} = 3.26$, $P = 0.0449$	
Fertility (% egg hatch)		
Greenbug	42.4 ± 4.2bB	65.8 ± 3.9aA
Flour moth	68.8 ± 5.4aA	68.1 ± 3.7aA
Pollen	49.1 ± 6.6bA	46.7 ± 6.6bA
	$F_{2,66} = 5.13$, $P = 0.0085$	
Fertility (no. larvae/female)		
Greenbug	58.0 ± 10.8bB	108.1 ± 10.2aA
Flour moth	129.4 ± 13.9aA	101.1 ± 9.6aA
Pollen	66.8 ± 17.1bA	50.3 ± 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

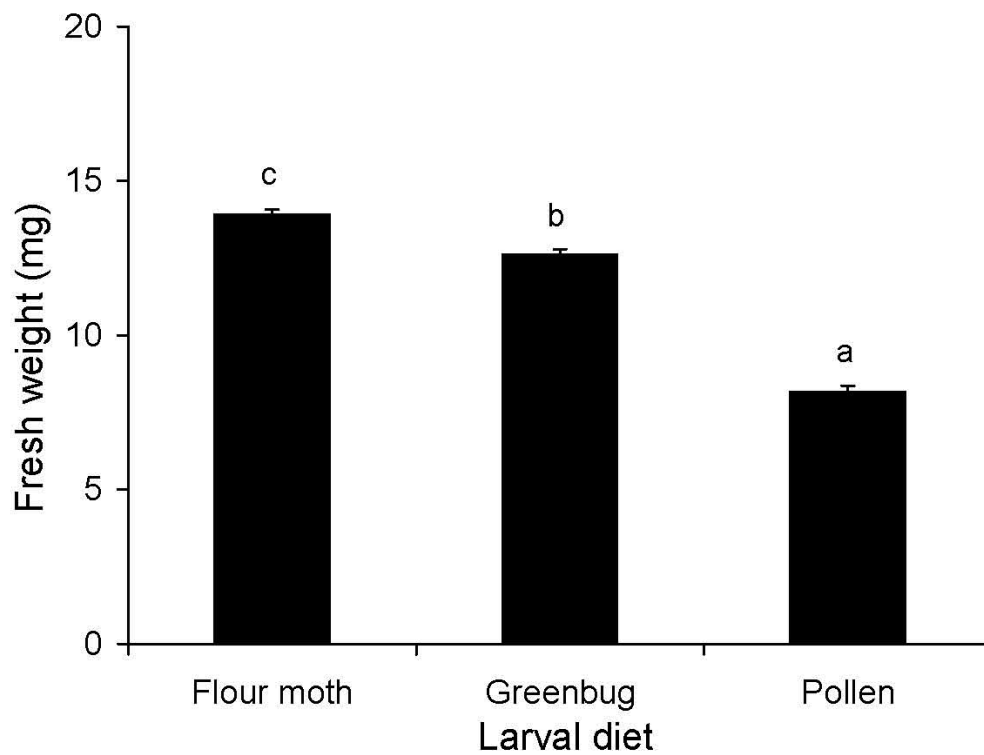407 significantly different ($\alpha > 0.05$).

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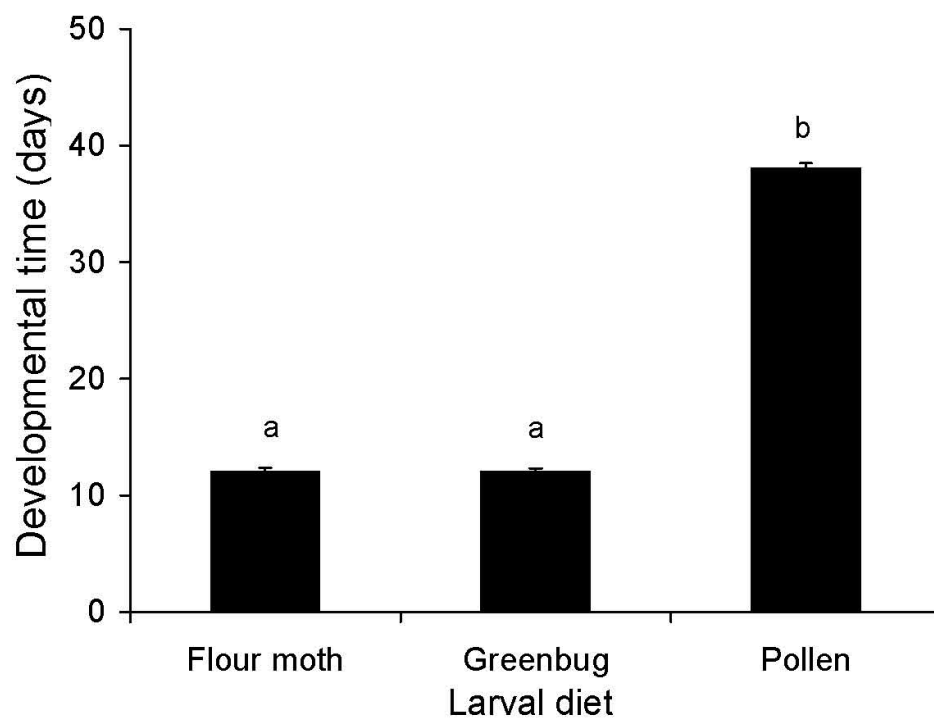
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412   **Fig.2.** Mean (+ SEM) fresh emergence weights of *Coleomegilla maculata* adults reared

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 ($\alpha > 0.05$).

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