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

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Abstract

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

Introduction

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

Although herbivorous insects tend to demonstrate strong consistencies between larval and adult food plants, insects that are predaceous as both larva and adult may not necessarily feed on the same prey in both life stages. For example, Murdoch (1969) demonstrated that foraging predators may switch among prey types to concentrate on those that are most abundant. However, surprisingly few studies have addressed the possible consequences of mixed diets or prey switching in predatory insects. Soares et al. (2004) examined effects of mixed diets on the adult performance of *Harmonia axyridis* Pallas, but did not test for effects across life stages. Hauge et al. (1998) found that *Coccinella septempunctata* L. raised on a mixed diet of

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three aphid species were intermediate in developmental time and adult weight to individuals raised on single aphid species that varied in suitability as prey, but they did not evaluate adult reproductive performance. Hattingh & Samways (1992) found that a change in prey during the larval stage had adverse consequences for the development of two *Chilocorus* spp., and that a change in adult diet caused temporary reductions in female reproductive performance, but they did not test for interactions between larval and adult diets. Other studies have tested the effects of mixed vs. monotypic diets in generalist predators, such as carabid beetles (Jorgensen & Toft, 1997; Fawki & Toft, 2005; Toft, 2005) and spiders (Oelbermann & Scheu, 2002; Allard & Yeargan, 2005) with somewhat mixed results.

The 12-spotted lady beetle, *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae), is a relatively polyphagous coccinellid species and, consequently, is one of the easiest to rear on factitious diets (Hodek & Honek, 1996). Unlike other primarily aphidophagous species, *C. maculata* can complete development on a diet of pollen without any source of animal protein, although the period of development is substantially increased and adult size reduced (Lundgren & Weidenmann, 2004; Michaud & Grant, 2005). It is also known to feed regularly on the eggs of various Lepidoptera (Phoofolo et al., 2001; Pfannenstiel & Yeargen, 2002; Musser & Shelton, 2003). The polyphagous habits of this species render it eminently well suited for exploration of larval–adult diet interactions because viable adults can be reared on larval diets that vary greatly in suitability.

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

Materials and methods

Insect colony

A colony of *C. maculata* was established from adult beetles collected from maize plants in Hays, KS, USA, in early May, 2006. All insect life stages were held in a growth chamber with L16:D8 day length at a temperature of 24 ± 1 °C. Adult females were isolated in plastic Petri dishes (5.5 cm in diameter) and were fed a diet of frozen eggs of the flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) (Beneficial Insectary, 14751 Oak Run Road, Oak Run, CA, USA), with water provided on a small cube of sponge, both refreshed every 2nd day. All insects used in experiments were only one generation removed from field-collected adults. Egg clusters, typically laid on inner surfaces of the Petri dishes, were collected daily by transferring the beetles to new dishes, or simply switching the lids. Egg clusters were held for 4 days until eclosion of larvae. Larvae of the first laboratory generation were reared on frozen eggs of *E. kuehniella* and offspring of the resulting adults were used in the experiment.

Experimental design

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

Data collection

As females became reproductive, we collected and counted their egg clusters daily and recorded the number of eggs that subsequently hatched until we had collected a total of 12 days of reproduction from each female. As the bulk of female reproductive effort occurs during the first weeks of reproductive life (Dixon & Agarwala, 2002), it is not necessary to collect lifetime fecundity in order to evaluate effects of diet on reproductive performance (Michaud, 2005; Michaud & Grant, 2005). We calculated the pre-reproductive period of each female as the number of days from adult emergence until production of its first egg cluster, and the reproductive period as the number of days required to achieve 12 days of oviposition. Fecundity was tallied as the total number of eggs laid in 12 days of reproduction. Fertility was estimated in two ways; by the percentage of eggs that hatched for each female, and by the number of larvae produced per female.

Statistical analysis

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

Results

Development

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

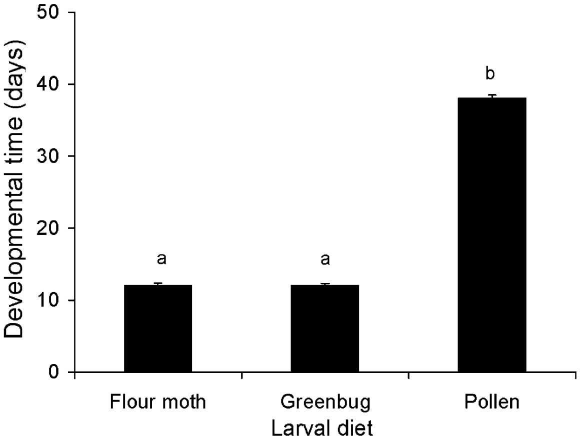

Figure 1 Mean (+ SEM) developmental times (from eclosion to formation of a pre-pupa) of *Coleomegilla maculata* larvae reared on (i) eggs of *Ephestia kuehniella*, (ii) greenbug, *Schizaphis graminum*, and (iii) bee pollen. Columns capped with the same letter were not significantly different ($\alpha>0.05$).

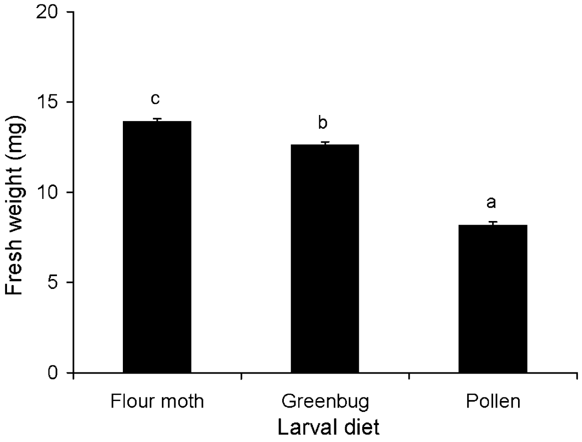

Figure 2 Mean (+ SEM) fresh emergence weights of *Coleomegilla maculata* adults reared on (i) eggs of *Ephestia kuehniella*, (ii) greenbug, *Schizaphis graminum*, and (iii) bee pollen. Columns capped with the same letter were not significantly different ($\alpha>0.05$).

Reproduction

We obtained a total of 12 days of reproduction from 15 females in the greenbug–greenbug treatment, 17 females in the greenbug–flour moth treatment, nine females in the flour moth–greenbug treatment, 19 females in the flour moth–flour moth treatment, six females in the pollen–greenbug treatment, and six females in the pollen–flour moth treatment. Data for reproductive period, fecundity, and fertility are reported in Table 1. The pre-reproductive period averaged 14.8 ± 1.1 days and did not vary significantly as a function of diet. When greenbug was the larval diet, adult females required fewer days to produce 12 clutches and had significantly higher fertility (both measures) when fed with moth eggs than when fed with greenbug, but did not differ in fecundity. When moth eggs were the larval diet, adult females fed greenbug had higher fecundity than those fed moth eggs, whereas other measures of performance did not differ between adult diets. When pollen was the larval diet, adult females did not differ in any measure of performance between adult diets.

When the adult diet was greenbug, the larval diet of moth eggs resulted in higher fecundity and fertility than either greenbug or pollen (Table 1). When moth eggs were

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

	Adult diet	
Larval 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 (number of 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 (percentage of 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 (number of 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	

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

the adult diet, adult females reared on pollen had lower fecundity and fertility than those reared on greenbug or moth eggs, and females reared on greenbug produced 12 clutches in a shorter period than those fed moth eggs or pollen.

Discussion

Michaud (2005) argued that prey suitability may differ for larval and adult coccinellids and should be evaluated separately. Adult coccinellids have stronger mandibles and more highly developed digestive systems than do larvae and likely process some types of food more efficiently. For example, coccinellid larvae typically suck the body contents of aphids leaving an empty shell, whereas adults consume whole aphids, including the cuticle, such that a careful examination of gut contents can be used to identify prey types (Mendel et al., 1985). Furthermore, larvae utilize resources for growth and development, whereas adults use them for dispersal and reproduction, and the nutritional demands of these various functions may differ. The present findings underline the importance of assessing prey suitability separately for adults and larvae when species are predatory in both life stages, and the importance of considering possible interactions between larval and adult diets.

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

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

Larvae of *C. maculata* fed exclusively pollen experienced delayed development and substantially reduced adult weight (Figure 1), which is consistent with previous observations of this species (Lundgren & Weidenmann, 2004; Michaud & Grant, 2005). The negative relationship between developmental time and adult weight in coccinellids is well-recognized (Dixon, 2000). Similarly, Tarango & Quiñones (2001) showed that developmental time of *Harmonia axyridis* Pallas was lengthened as daily food rations were reduced. Thus, protracted periods of development in coccinellids may compensate for either reduced food quantity or reduced food quality. Dixon (2000) reasoned that aphidophagous lady beetles develop as fast as possible for such insects, and in parallel with the fast development of their aphid prey. Aphid colonies represent highly ephemeral resources that can be very abundant, but only for short periods. Under these conditions, rapid development of larvae is advantageous and selection may favor mechanisms that couple increases in developmental rate with increases in growth rate such that fast development does not exact a cost in terms of adult body size.

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

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

Legacies of larval experience on adult behavior, such as those observed in aphid parasitoids (Wickremasinghe & van Emden, 1992; Storeck et al., 2000; Douloumpaka & van Emden, 2003), typically guide adults to the same plants that harbored the larval host, and presumably the same host species. Possible legacy effects of larval prey plants have not yet been tested in coccinellids, but we suspect that such mechanisms are adaptive only for species that are relatively short lived, develop quickly, and have limited dispersal ability. Such insects are more likely to benefit from host- or prey-plant fidelity than those longer lived, more polyphagous species that frequently experience changes in prey availability within the time frame of a single generation.

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

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