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Three Homopteran Pests of Citrus as Prey for the Convergent Lady Beetle: Suitability and Preference

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ABSTRACT The convergent lady beetle, *Hippodamia convergens* Guérin-Ménéville (Coleoptera: Coccinellidae), is an important predator of soft-bodied insect pests in many regions of the United States, but generally uncommon in Florida citrus. Certain citrus producers in Florida recently initiated releases of commercially available *H. convergens* from California against the Asian citrus psyllid *Diaphorina citri* Kuwayama, vector of Huanglongbing or citrus greening disease. However, there is little information on potential efficacy of this predator against the psyllid or other pests of citrus. Preference, development, and reproduction by *H. convergens* was evaluated on freshly collected nymphs of *D. citri*, brown citrus aphid *Toxoptera citricida* Kirkaldy, green citrus aphid *Aphis spiraecola* Patch, and frozen eggs of the flour moth *Ephesthia kuehniella* Zeller. Larvae preferred *D. citri* over *T. citricida* in two-way choice tests and consumed more *D. citri* or *A. spiraecola* than *T. citricida* in no-choice tests. Adults consumed equal numbers of all three species in both tests. Development times of larvae at $25.5 \pm 0.05^\circ\text{C}$ on *A. spiraecola* were longer than on the other three diets. Larval survival and pupation times did not differ among diets. Females lived longer than males irrespective of diet, and longevity of both genders was greatly increased on *E. kuehniella* compared with *D. citri* and *A. spiraecola*. Life table analysis indicated that *H. convergens* should increase on all three species, with a greater potential on psyllids than aphids. Further studies are warranted to assess establishment and persistence of this potential biological control agent in the Florida citrus environment.

KEY WORDS Asian citrus psyllid, biological control, Huanglongbing, life table, *Candidatus liberibacter asiaticus*

Diaphorina citri Kuwayama (Homoptera: Psyllidae), commonly known as the Asian citrus psyllid, *Toxoptera citricida* Kirkaldy (Homoptera: Aphididae), commonly known as the brown citrus aphid and *Aphis spiraecola* Patch (Homoptera: Aphididae), commonly known as the green citrus aphid or spirea aphid, are all important insect pests of citrus in Florida and elsewhere. The pest status of both *D. citri* and *T. citricida* is largely because of their roles as vectors of two devastating diseases of citrus. *Diaphorina citri* vectors *Candidatus liberibacter asiaticus* the causal agent of Huanglongbing (HLB) or citrus greening disease (Garnier et al. 2000, Bové 2006). *Toxoptera citricida* vectors citrus tristeza virus (CTV) responsible for the death of millions of trees on sour orange rootstock (Balaraman and Ramakrishnan 1979, Yokomi and Damsteegt 1991).

Both *T. citricida* and *D. citri* are invasive pests first detected in Florida in 1995 and 1998, respectively, whereas *A. spiraecola* has been present since at least 1923 (Halbert 1997, 1998; Miller 1929). All three are common in Florida citrus, although *D. citri* has be-

come the prime target of control efforts because of the recent spread of HLB throughout the state (<http://www.freshfromflorida.com/pi/chrp/greening/citrusgreening.html>). Biological control is an important component of citrus pest management in Florida including psyllids and aphids (McCoy 1985, Michaud 1999, 2004; Qureshi and Stansley 2009). Enhancement of biological control in Florida citrus through augmentation of species specific parasitoids and generalist predators may contribute to reduction in incidence of psyllids and aphids and the diseases they spread. However, parasitism is usually only a minor source of mortality for these aphid species. The native *Lysiphlebus testaceipes* Cresson (Hymenoptera: Aphididae) only occasionally contributes appreciable mortality to *T. citricida* (Michaud 1999). *Tamarixia radiata* (Waterston) (Hymenoptera: Eulophidae), is the only one of two introduced parasitoids of *D. citri* that is well established in Florida, but has yet to contribute significant mortality to populations of *D. citri* there (Michaud 2004, Qureshi et al. 2009, Qureshi and Stansley 2009).

In contrast to the parasitoids, predacious arthropods, particularly the coccinellid species *Olla v-nigrum* (Mulsant), *Curinus coeruleus* (Mulsant), *Har-*

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monia axyridis (Pallas) and *Cycloneda sanguinea* (L.) contribute significantly to the natural mortality of aphids and psyllids in Florida citrus (Michaud 1999, 2004; Qureshi and Stansly 2009). None of these species are commercially available for mass release. However, strategies to conserve their natural populations are being developed (Qureshi and Stansly 2009, 2010).

The convergent lady beetle, *Hippodamia convergens* Guérin-Ménéville (Coleoptera: Coccinellidae), is an important predator of soft-bodied pests such as aphids, scales and mites, particularly in cereal crops (Nechols and Harvey 1998, Michels et al. 2001, Michaud and Qureshi 2005). We did not observe this species in citrus groves during several of our studies through 2008, nor have we found any reports of its appearance in Florida citrus in response to the recent invasions of *T. citricida* and *D. citri* (Qureshi and Stansly 2008, 2009, 2010). This species was not cited as a predator of *D. citri* by Michaud (2004) although it earlier was included as a minor element of the coccinellid fauna observed on Florida citrus (Michaud 2000). It was abundant in a study of coccinellids on citrus in Puerto Rico (Pluke et al. 2005), but this population may be genetically distinct from those on the U.S. mainland as a result of different selection pressures.

Hippodamia convergens is one of the most commonly used natural enemies in North America (van Lenteren 2003). Billions of adults are collected annually from their overwintering sites in the Sierra Nevada Mountains of southern California and sold for mass release to commercial growers and home gardeners throughout the United States and Canada (Obrycki and Kring 1998). However, no information is available from California on the possible role of *H. convergens* in suppression of *D. citri*, probably because of the recent discovery of this pest in the state and an aggressive campaign of insecticidal control. Nevertheless, certain citrus producers in Florida initiated releases of commercially available *H. convergens* beetles in 2008 with the aim of aiding control efforts against *D. citri*. ≈ 1.5 million individuals, presumably collected from hibernacula in California, were released in April 2008 in three commercial groves, two in Lake Wales, FL and one in Haines City, FL. Several million were also released in commercial groves in Collier Co., Florida multiple times during the spring and summer of 2009 and 2010. Objectives of such releases may have been temporary inundation to provide immediate reduction of the target pest, augmentation of newly established populations, or permanent establishment of a new strain of *H. convergens*. However, it was yet uncertain that these beetles will establish in Florida citrus groves, reduce pest populations or even feed on the intended prey, given that they originated in a habitat devoid of *D. citri*.

Michaud (2000) studied development and reproduction of *H. convergens* from Florida on *T. citricida* and *A. spiraeola* but not on *D. citri*. Again, this population may have been genetically distinct from California populations due to different selection pressures. Therefore, the primary rationale for this work was to evaluate prey suitability of California *H. con-*

vergens, given that it was being released in Florida without information on potential efficacy against the primary target pest, *D. citri* or *T. citricida* or *A. spiraeola*. We conducted experiments to (a) test the preference of larvae and adults of *H. convergens* for nymphs of *D. citri*, *T. citricida* or *A. spiraeola* and (b) evaluate survival, development, and reproduction of *H. convergens* on these three diets and on frozen eggs of the flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). *Ephestia* was included as reference diet because it was known to support the development and reproduction of several lady beetle species (Michaud and Olsen 2004).

Materials and Methods

Stock Colony of *H. convergens*. A laboratory colony of *H. convergens* was established at the Southwest Florida Research and Education Center (SWFREC), Immokalee, FL in July 2009 from adults collected in a commercial citrus grove in Collier County where beetles from California had been released. The colony was maintained in an incubator (phEnvironmental, model CEC 23LTP, Harris Manufacturing Company, North Billerica, MA) set to a photoperiod of 16:8 (L:D) hours at 24°C under 'cool white' fluorescent lightning. Both adults and larvae were reared on an *ad libitum* supply of frozen *E. kuehniella* eggs (Beneficial Insectary, 9664 Tanqueray Ct. Redding, CA 96003 and Koppert Biological Systems, Romulus MI 48174) provided every Monday, Wednesday and Friday. Larvae were reared individually in plastic petri dishes (9 cm diameter by 1.5 cm high) and provided with water on a small cube of sponge. Adults were reared in groups of 10–15 in 2-liter ventilated plastic jars covered with a muslin cloth. Water was provided on a cotton wick fixed in a small plastic cup glued to the base of the jar. Beetles were provided untreated citrus shoots as substrate for oviposition. Shoots were replaced on the days that food was provided and eggs were collected and kept in petri dishes. Upon eclosion, larvae were separated into petri dishes, one per dish, using a soft camel's-hair brush and reared to adulthood on frozen eggs of *E. kuehniella*.

Choice and No-choice Tests. Experiments were designed as randomized complete blocks and conducted in an incubator under conditions described for stock colony. Starved neonates (48 h old) of *H. convergens* were offered small and large nymphs of *D. citri*, *T. citricida* and *A. spiraeola* in choice and no-choice tests. Size rather than instar was used to standardize prey because of differences in body mass within the same instar of the three species. However, the small size group generally consisted of second and third instars and the large size group of fourth and fifth instars. Psyllids and aphids used in these experiments were collected from untreated citrus trees in a commercial organic orchard in Lake Wales, FL.

Experimental arenas consisted of plastic petri dishes (9 cm by 1.5 cm) containing no other material but nymphs of the test species. Choice tests with small size nymphs evaluated *D. citri* versus *T. citricida*, *D. citri*

versus *A. spiraeicola* and *T. citricida* versus *A. spiraeicola*. The larva in each petri dish was provided with five nymphs of each of the two test species for a total of 10 nymphs. Twenty four larvae were randomly distributed across three prey combinations in four replicates. Each replicate was placed in a plastic tray (3 cm by 26 cm by 52 cm) on a separate shelf of the incubator. A simultaneous no-choice test was conducted using the same conditions and procedures except that the larva in each petri dish was provided with 10 nymphs of the same species instead of five nymphs of each of two species. Both choice and no-choice tests were conducted using two backgrounds at the same time by placing half of the test arenas in each replicate on a white sheet of paper and half on a dark green sheet. This was done to control for differences in background contrast between the test species, which could possibly influence predator encounter and attack behavior (Harmon et al. 1998, Michaud 2000).

Procedures for choice and no-choice experiments conducted to test larvae and adults of *H. convergens* against large size nymphs of the same three species were similar to those described for small size nymphs, except that satiated adults from the stock colony were separated into individual petri dishes and starved for 24 h to maximize their motivation to forage (Frazer and Gilbert 1976). Evaluations of consumption rates were made when a substantial number of both prey types were still present, i.e., at 6 h for larvae versus small nymphs, 6 and 18 h for larvae versus large nymphs, and 3 and 6 h for adults versus large nymphs.

Development and Reproduction of *H. convergens*. Multiple egg batches of *H. convergens* were collected from the stock colony and held in plastic petri dishes under conditions described for stock colony. Larvae were separated one each into petri dishes within 12 h of hatching. Thirty six larvae were assigned to diets of *E. kuehniella*, *D. citri*, *T. citricida* and *A. spiraeicola* in three replicates in a randomized complete block design. Each replicate was placed on a separate shelf of the incubator. An *ad libitum* supply of frozen eggs of *E. kuehniella* or freshly collected nymphs of *D. citri*, *T. citricida* and *A. spiraeicola* was provided daily to larvae in respective treatments until death or pupation. Shoots containing psyllids and aphids were collected from untreated citrus trees at SWFREC and a neighboring commercial grove. Shoots were carefully examined before they were provided to the larvae to remove any other pests or predators, thus ensuring that only the desired prey species was offered. Eggs of *E. kuehniella* were provided on a clean citrus leaf. Larvae were transferred to clean petri dishes every other day. Water was provided on a small cube of sponge. Dates of larval mortality, pupation and adult emergence were recorded.

Two experiments were conducted to assess reproduction of *H. convergens* on different prey. In the first experiment, 50 neonates were reared individually in plastic petri dishes on *ad libitum* supplies of frozen eggs of *E. kuehniella* and water provided every other day. Within 24–48 h of eclosion from pupae, adults that had not been exposed to any diet were released

in a 3-liter ventilated plastic jar covered with the muslin cloth and observed continuously for mating. Mating began within a few hours and mating pairs were isolated as they formed and transferred to petri dishes (9 cm by 1.5 cm). In total, 12 pairs were isolated and distributed at random across three diets consisting of frozen eggs of *E. kuehniella* or freshly collected nymphs of *D. citri* or *A. spiraeicola*. Four replicates and randomized complete block design was used. Temperature and relative humidity averaged $25.5 \pm 0.05^\circ\text{C}$ and $63 \pm 0.2\%$, respectively during larval development and $27.3 \pm 0.03^\circ\text{C}$ and $64 \pm 0.2\%$, respectively during the adult stage. *Toxoptera citricida* was not included in this experiment because insufficient numbers were available to maintain a continuous supply of this species throughout the life of the beetles.

Beetles were provisioned with an *ad libitum* supply of their respective diets every other day. Psyllids and aphids were provided on citrus shoots collected from the same locations and treated as described for larval development. A small piece of folded paper towel was added to each petri dish as an additional substrate for oviposition. Water was provided as on a small cube of sponge. Petri dishes and all other substrates were checked daily for oviposition. Eggs were counted and removed, along with the material on which they were laid and incubated in a separate petri dish under conditions described for stock colony. Petri dishes with beetles were replaced every other day or earlier if eggs were laid on the dish. Newly hatched larvae were removed every day with a soft camel's-hair brush to avoid cannibalism of remaining eggs. Dates of beetle death were recorded.

A second experiment to assess reproduction of *H. convergens* was conducted for 6 wk with five to eight replicates using *T. citricida* and three diets evaluated in the first experiment. Experimental conditions and procedures were similar to the first experiment.

Statistical Analysis. We used generalized linear models with Poisson errors (PROC GENMOD) at $P = 0.05$ to discern differences in number of nymphs of different species consumed by larvae and adults in each experiment (SAS Institute 2004). Data from no-choice tests were used to analyze the effect of white and dark green backgrounds of the experimental arena on the consumption rate of larvae and adults. Data on larval survival until pupation or adult eclosion were analyzed by using the GLIMMIX MACRO model with a logit link function to transform data (SAS Institute 2004). The analysis involves a mixed model analysis of variance (ANOVA), with a binomial error structure (Littell et al. 1996). Larval development times (days), pupation times (days), adult longevity (days), cumulative fecundity (number of eggs per female), and cumulative fertility (percentage of egg hatch and number of larvae per female), were compared across diets using the GLM procedure and the least significant difference (LSD) test for separation of treatment means ($P = 0.05$). The Shapiro Wilk W test ($P = 0.05$) and observations of normality plots indicated that data satisfied assumptions of parametric analysis (Shapiro and Wilk 1965, Shapiro et al. 1968). Repeated-meas-

Table 1. Mean number ($\pm$ SEM) of small (2–3 instar) and large (4–5 instar) nymphs of *Diaphorina citri*, *Toxoptera citricida*, and *Aphis spiraeicola* consumed by larvae and adults of *Hippodamia convergens* in two-way choice and no-choice tests

Insect development stage	Choice tests			No-choice tests		
	<i>D. citri</i>	<i>T. citricida</i>	<i>A. spiraeicola</i>	<i>D. citri</i>	<i>T. citricida</i>	<i>A. spiraeicola</i>
	6 h			6 h		
Larvae vs small nymphs	2.13 $\pm$ 0.44	1.13 $\pm$ 0.30	—	6.13 $\pm$ 0.48a	3.88 $\pm$ 0.72b	7.00 $\pm$ 0.76a
Larvae vs small nymphs	1.88 $\pm$ 0.23	—	2.13 $\pm$ 0.23	—	—	—
Larvae vs small nymphs	—	1.88 $\pm$ 0.40	2.00 $\pm$ 0.27	—	—	—
Larvae vs large nymphs	0.87 $\pm$ 0.30a	0.13 $\pm$ 0.13b	—	1.50 $\pm$ 0.19	0.75 $\pm$ 0.16	0.88 $\pm$ 0.13
Larvae vs large nymphs	0.88 $\pm$ 0.23	—	0.63 $\pm$ 0.26	—	—	—
Larvae vs large nymphs	—	0.50 $\pm$ 0.27	0.88 $\pm$ 0.23	—	—	—
	3 h			3 h		
Adult vs large nymphs	2.38 $\pm$ 0.38	2.63 $\pm$ 0.32	—	4.38 $\pm$ 0.38	5.00 $\pm$ 0.33	4.50 $\pm$ 0.50
Adult vs large nymphs	2.63 $\pm$ 0.46	—	3.00 $\pm$ 0.53	—	—	—
Adult vs large nymphs	—	3.38 $\pm$ 0.42	1.88 $\pm$ 0.30	—	—	—

Larvae were newly eclosed first instars and were not exposed to any diet before the tests. Adults were collected from the the laboratory reared stock colony on frozen eggs of *Ephestia kuehniella* and were starved for 24 h before the tests. Means in the same row and time exposure followed by the same letter or no letter were not significantly different ($P > 0.05$).

tures ANOVA was used to test the effect of diet on fecundity and fertility ($P = 0.05$) through week seven (first experiment) or six (second experiment) using GLM and MIXED model procedures, respectively (SAS Institute 2004). The MIXED procedure was used for egg hatch data because weeks when no eggs were laid were treated as missing values. Data are reported as Means $\pm$ SE. Survival and fecundity data on the four diets given a sex ratio of 1:1 were used to estimate demographic parameters for *H. convergens* using a Jackknife procedure (Maia et al. 2000, SAS Institute 2004). Pairwise comparisons of the parameters between diets were made using Student's *t*-test.

Results

Choice and No-choice Tests. No effect of background color was observed on consumption rate of larvae or adults with any of the three prey species tested in no-choice experiments ($P > 0.05$), so data were pooled for further analysis. Larvae consumed more *D. citri* than *T. citricida* at 6 h in choice tests with large nymphs ($\chi^2 = 5.1$, $df = 1$, $P = 0.025$, Table 1). A similar trend was observed for small nymphs of these two species, although the treatment effect was not statistically significant. There were no other significant differences in larval consumption of nymphs at 6 h or adult consumption of large nymphs at 3 h. There were also no significant differences in consumption of large nymphs between any two prey species ($P > 0.05$) by larvae at 18 h (38–48%) or adults at 6 h (60–95%) (data not presented).

In no-choice tests, larval consumption of small nymphs of the three species differed at 6 h ($\chi^2 = 7.7$, $df = 2$, $P = 0.021$, Table 1). Fewer *T. citricida* were consumed than *D. citri* ($\chi^2 = 4.0$, $df = 1$, $P = 0.046$) or *A. spiraeicola* ($\chi^2 = 7.0$, $df = 1$, $P = 0.008$) but no differences were observed between *D. citri* and *A. spiraeicola* ($P > 0.05$). There were no significant differences in consumption of large nymphs by larvae at six or 18 h or adults at 3 or 6 h (data not presented for larvae at 18 h and adults at 6 h).

Development and Reproduction. Larval survival until pupation or adult eclosion did not differ among the four diets ($P > 0.05$, Table 2). However, development time was prolonged on *A. spiraeicola* compared with the other three diets ($F = 4.9$, $df = 3, 16$, $P = 0.014$, Table 2), which did not differ from each other ($P > 0.05$). There was no significant effect of diets on pupation time ($P > 0.05$, Table 2).

Longevity of both males and females was reduced on diets of *D. citri* or *A. spiraeicola* compared with *E. kuehniella* (Males: $F = 42.88$, $df = 2, 6$, $P < 0.001$; Females: $F = 13.59$, $df = 2, 6$, $P = 0.006$; Table 3), with no difference between *D. citri* and *A. spiraeicola* ($P > 0.05$, Table 3). Females (83%) on all three diets began ovipositing within 1 wk of eclosion and first mating. Most females (87.5%) on *D. citri* or *A. spiraeicola* lived and oviposited for seven weeks, whereas females on *E. kuehniella* lived and reproduced for more than 20 wk. Therefore, fecundity and fertility data were compared for the first 7 wk and for the entire female lifetime.

In total, 199 oviposition events were observed of which 39.7% occurred on leaves, followed by 29.6% on

Table 2. Mean ($\pm$ SEM) survival, development times, and pupation times of *Hippodamia convergens* on diets of *Ephestia kuehniella*, *Diaphorina citri*, *Toxoptera citricida*, and *Aphis spiraeicola*

Diet	Larvae surviving to pupae (%)	Larvae surviving to adult (%)	Development times of larvae pupating (days)	Pupation times (days)
<i>E. kuehniella</i>	77.8 $\pm$ 22.2	77.8 $\pm$ 22.2	8.0 $\pm$ 0.0b	4.3 $\pm$ 0.4
<i>D. citri</i>	55.6 $\pm$ 11.1	44.4 $\pm$ 11.1	8.8 $\pm$ 0.8b	5.0 $\pm$ 0.0
<i>T. citricida</i>	44.4 $\pm$ 29.4	44.4 $\pm$ 29.4	8.5 $\pm$ 0.3b	5.3 $\pm$ 0.6
<i>A. spiraeicola</i>	66.7 $\pm$ 19.3	33.3 $\pm$ 19.3	11.5 $\pm$ 0.9a	5.0 $\pm$ 0.1

Means within a column followed by the same letter or no letter were not significantly different ($P > 0.05$).

Table 3. Adult longevity and reproductive performance of *Hippodamia convergens* on diets of *Ephestia kuehniella*, *Diaphorina citri*, and *Aphis spiraeicola* (first exp, *T. citricida* not included)

Diet	Male longevity (days)	Female longevity (days)	Fecundity (no. of eggs/female)		Fertility (percentage of egg hatch)		Fertility (no. of larvae/female)	
			First seven weeks		First seven weeks		First seven weeks	
			Mean $\pm$ SEM	Lifetime	Mean $\pm$ SEM	Lifetime	Mean $\pm$ SEM	Lifetime
<i>E. kuehniella</i>	Mean $\pm$ SEM	Mean $\pm$ SEM	Mean $\pm$ SEM	Mean $\pm$ SEM	Mean $\pm$ SEM	Mean $\pm$ SEM	Mean $\pm$ SEM	Mean $\pm$ SEM
	118.75 $\pm$ 7.22a	157.00 $\pm$ 12.42a	85.00 $\pm$ 51.48	259.50 $\pm$ 83.14	94.13 $\pm$ 4.69a	58.55 $\pm$ 20.79	101.00 $\pm$ 49.73	109.00 $\pm$ 50.59
<i>D. citri</i>	41.50 $\pm$ 6.51b	60.50 $\pm$ 4.37b	218.75 $\pm$ 13.91	219.75 $\pm$ 14.90	84.35 $\pm$ 3.05a	84.14 $\pm$ 3.15	184.00 $\pm$ 10.35	184.25 $\pm$ 10.55
<i>A. spiraeicola</i>	44.50 $\pm$ 2.90b	70.50 $\pm$ 17.21b	315.25 $\pm$ 66.30	315.25 $\pm$ 66.30	56.52 $\pm$ 8.99b	56.52 $\pm$ 8.99	167.50 $\pm$ 35.23	167.50 $\pm$ 35.23

Means within a column followed by the same letter or no letter were not significantly different ($P > 0.05$).

the petri dish, 26.6% on paper towel, and 4% on the sponge. A significant diet-by-week interaction ($F = 2.8$, $df = 12$, 54 , $P = 0.005$) on fecundity of *H. convergens* was observed in the first experiment, which included diets of *D. citri*, *A. spiraeicola*, and *E. kuehniella*. Fewer eggs were laid by beetles feeding on *E. kuehniella* compared with diets of *D. citri* or *A. spiraeicola* during weeks four ($F = 10.7$, $df = 2$, 9 , $P = 0.004$, Fig. 1A) and five ($F = 11.9$, $df = 2$, 9 , $P = 0.003$, Fig. 1A) with no differences between *D. citri* or *A. spiraeicola* ($P > 0.05$). The same trend was seen over seven weeks but not the full lifetime because of greater longevity on *E. kuehniella*. Diet had a significant ($F = 17.1$, $df = 2$, 5 , $P = 0.006$) effect on fertility, with only 57% eggs hatching from females fed on *A. spiraeicola* compared with 84 and 94%, respectively, from *D. citri* or *E. kuehniella*, which did not differ. These compensating effects tended to diminish differences in production of live larvae which was not significantly different among treatments after 7 wk or over the lifetime, with diet-by-week interactions on egg hatch or number of larvae per female also not significant ($P > 0.05$).

In the second experiment, which included *T. citricida*, a significant diet-by-week interaction on fecundity was again observed ($F = 2.4$, $df = 15$, 95 , $P = 0.007$). Fewer eggs were laid on a diet of *E. kuehniella* than *D. citri* or *T. citricida* in week two ($F = 4.7$, $df = 3$, 19 , $P = 0.013$, Fig. 1B) which did not differ from each other or from *A. spiraeicola* ($P > 0.05$). Fewer eggs were again laid on a diet of *E. kuehniella* in week three than with any of the three nymphal diets ($F = 4.1$, $df = 3$, 19 , $P = 0.020$, Fig. 1B), which did not differ from each other ($P > 0.05$). Overall, fewer eggs were laid on a diet of *E. kuehniella* than on the other three diets ($F = 5.9$, $df = 3$, 12 , $P = 0.010$, Table 4), which did not differ ($P > 0.05$). The diet-by-week interaction was significant on egg hatch ($F = 2.1$, $df = 15$, 76 , $P = 0.021$), with no hatch seen in week three on a diet of *E. kuehniella* compared with an average of 65% on the three nymphal diets ($F = 3.9$, $df = 3$, 13 , $P = 0.035$) which did not differ ($P > 0.05$). Over all weeks, an average of 70% egg hatch was observed with no differences among diets ($P > 0.05$, Table 4). The diet-by-week interaction was also significant on larvae produced per female ($F = 2.5$, $df = 15$, 35 , $P = 0.014$). More larvae were produced in week three on diets of *D. citri* or *T. citricida* (20–30 per female) compared with none on either *E. kuehniella* or *A. spiraeicola* ($F = 20.5$, $df = 3$, 7 , $P = 0.001$), with no difference between the former. Overall, females produced fewer larvae on a diet of *E. kuehniella* than the three nymphal diets ($F = 6.4$, $df = 3$, 12 , $P = 0.008$; Table 4), which did not differ ($P > 0.05$).

Life Table Parameters. The greatest net reproductive rate (R_0) for *H. convergens* was estimated on a diet of *D. citri* although differences among diets were not statistically significant (Table 5). The intrinsic rate of increase (r_m) and the finite rate of increase (λ) were both greatest on a diet of *D. citri* with significant differences compared with diets of *A. spiraeicola* or *T. citricida*. Mean generation time (T) and doubling time (Dt) were least on a diet of *D. citri*. The difference in

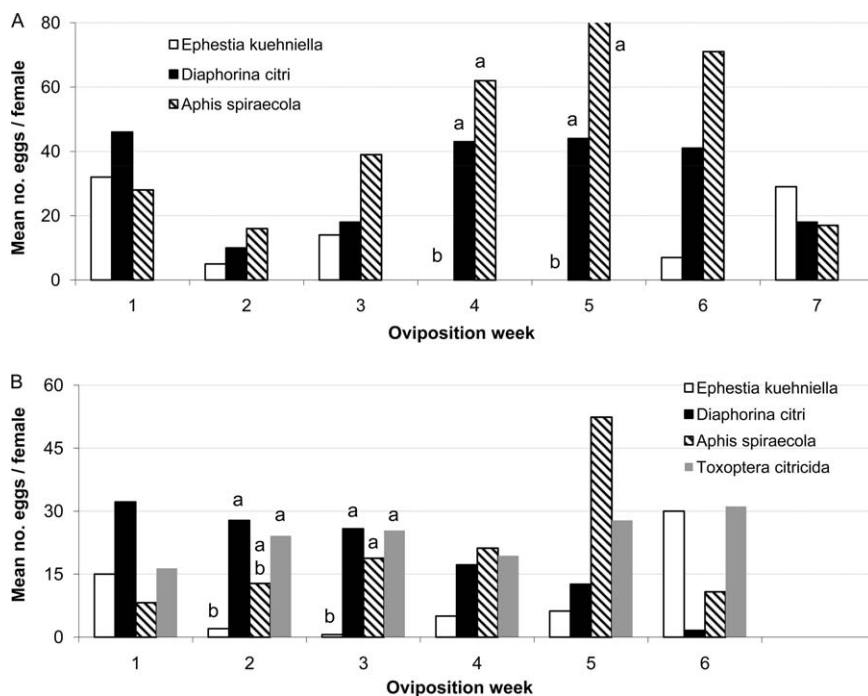


Fig. 1. Fecundity of *H. convergens* during the first seven (A, first experiment) or six (B, second experiment) weeks of life on diets of *E. kuehniella*, *D. citri*, *A. spiraeicola*, and *T. citricida* (second experiment only). Means within oviposition weeks followed by the same letter or no letter were not significantly different ($P > 0.05$).

T was significant compared with *A. spiraeicola* and in *Dt* compared with both *A. spiraeicola* and *T. citricida*.

Discussion

Greater consumption by larvae of *H. convergens* of *D. citri* compared with *T. citricida* in both choice and no-choice tests indicated preference for *D. citri* over *T. citricida*. Larval preference for *D. citri* may be caused by attraction to volatiles, color, or perception of the nutritional value of the prey, and needs further investigation. In contrast, adults showed no preference between psyllids and aphids, a finding similar to Pluke et al. (2005).

There was no difference in larval survival of *H. convergens* on four diets. However, only 50% of beetles emerged from pupae that developed on a diet of *A. spiraeicola*, thus reducing survival from 66.7 to 33.3%. Development times of larvae were indistinguishable on diets of *D. citri*, *T. citricida*, and *E. kuehniella* but were longer on *A. spiraeicola*. The results for develop-

ment times of Michaud (2000) of *H. convergens* from Florida on *T. citricida* and *A. spiraeicola* were similar to ours, although he observed that pupae from larvae that developed on *T. citricida* were small, malformed and did not yield adults.

Females lived longer than males irrespective of diet, and longevity of both genders increased significantly on *E. kuehniella* compared with *D. citri* and *A. spiraeicola*. However, fecundity was reduced on a diet of *Ephestia* eggs compared with all three nymphal diets during the first six to seven weeks of female life, indicating that more time was probably needed to mature eggs on the *Ephestia* diet. Reduced egg production would be expected to prolong survivorship of females, although male longevity was also prolonged on the *E. kuehniella* diet. Fertility was also reduced on a diet of *Ephestia* eggs compared with the three nymphal diets. Although the diet of *Ephestia* eggs has been found to be suitable for several species of coccinellids (Michaud 2004) and supported larval development of *H. convergens* in our study, it does not seem

Table 4. Mean ($\pm$ SEM) fecundity and fertility of *Hippodamia convergens* over 6 wk on diets of *Ephestia kuehniella*, *Diaphorina citri*, *Toxoptera citricida*, and *Aphis spiraeicola* (second experiment)

Diet	Fecundity (no. of eggs/female)	Fertility (percentage of egg hatch)	Fertility (no. of larvae/female)
<i>E. kuehniella</i>	58.80 $\pm$ 16.41b	64.92 $\pm$ 9.51	31.20 $\pm$ 9.33b
<i>D. citri</i>	117.20 $\pm$ 10.73a	78.13 $\pm$ 3.14	95.60 $\pm$ 7.00a
<i>T. citricida</i>	143.75 $\pm$ 20.21a	72.15 $\pm$ 6.42	100.88 $\pm$ 11.39a
<i>A. spiraeicola</i>	119.00 $\pm$ 21.10a	59.35 $\pm$ 11.01	72.80 $\pm$ 16.90a

Means within a column followed by the same letter or no letter were not significantly different ($P > 0.05$).

Table 5. Means and 95% CL of the life table parameters R_0 (net reproductive rate); r_m (intrinsic rate of increase); λ (finite rate of increase); T (generation time, days); and Dt (doubling time, days) of *Hippodamia convergens* on diets of *Ephestia kuehniella*, *Diaphorina citri*, *Toxoptera citricida*, and *Aphis spiraeicola* estimated using Jackknife procedure in SAS

Diet	R_0	95% CL	r_m	95% CL	λ	95% CL	T	95% CL	Dt	95% CL
<i>E. kuehniella</i>	23.11	7.09–39.13	0.18ab	0.08–0.28	1.19ab	1.08–1.31	17.28ab	8.68–25.87	3.67ab	1.07–6.27
<i>D. citri</i>	30.87	23.06–38.68	0.20a	0.17–0.23	1.22a	1.19–1.25	17.25b	14.25–20.25	3.48b	3.01–3.96
<i>T. citricida</i>	28.75	19.19–38.31	0.17b	0.14–0.19	1.18b	1.15–1.21	20.35ab	17.81–22.90	4.18a	3.60–4.76
<i>A. spiraeicola</i>	30.58	15.39–45.76	0.16b	0.14–0.18	1.17b	1.14–1.19	22.10a	19.62–24.59	4.44a	3.83–5.04

Means within a column followed by the same letter or no letter were not significantly different ($P > 0.05$).

to be ideal for optimal reproduction and fertility of this species. Similar impact of an *Ephestia* diet on reproduction of *H. convergens* was observed in another study that compared it to a diet of *Schizaphis graminum* Rondani, an aphid species that attacks cereal crops (Michaud and Qureshi 2005).

Fecundity and fertility of *H. convergens* was improved on *D. citri* and *T. citricida* compared with *A. spiraeicola*, a finding similar to Michaud (2000) although he only compared *T. citricida* and *A. spiraeicola*. Prolonged larval development that we observed on *A. spiraeicola* was another indication that this species is relatively inferior as a diet compared with *D. citri* and *T. citricida*. Furthermore, significantly greater r_m and λ that we estimated for *H. convergens* feeding on *D. citri* compared with either *A. spiraeicola* or *T. citricida* indicated greater potential for population increase on a psyllid diet compared with either aphid species. Greater net reproductive rate and shorter generation time both contributed to this difference.

The preference for *D. citri* by *H. convergens*, as well as the suitability of this prey for reproduction is surprising, given that the psyllid and coccinellid have only recently come into contact. Differences between our results and Michaud (2000) or Pluke et al. (2005) may be attributable to genetic differences among populations that manifested in prey use, dietary requirements, and climatic tolerance.

Our findings suggest that *D. citri*, *T. citricida*, and *A. spiraeicola* are all suitable prey for larvae and adults of *H. convergens* from California. Nevertheless, we still do not yet know how these beetles will respond to the Florida citrus environment. Therefore, field studies are warranted, not only to document the effectiveness and establishment of this species against psyllids and aphids in citrus, but to study interactions with already established species of lady beetles preying on psyllids and aphids, and the overall impact on populations of these and other arthropods in Florida citrus (Michaud 1999, 2004; Qureshi and Stansly 2009). In addition, the release of commercially available *H. convergens* from overwintering sites in California comes with the associated risk of importation of a variety of natural enemies as well as other arthropods and plant materials that may pose future ecological problems.

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