LADY BEETLES AS POTENTIAL PREDATORS OF THE ROOT WEEVIL *DIAPREPES ABBREVIATUS* (COLEOPTERA: CURCULIONIDAE) IN FLORIDA CITRUS

R. J. STUART, J. P. MICHAUD, L. OLSEN AND C. W. MCCOY
University of Florida, IFAS, Citrus Research and Education Center
700 Experiment Station Road, Lake Alfred, FL 33850

ABSTRACT

Diaprepes abbreviatus (L.) is a major pest of Florida citrus. Adult females lay eggs in masses sealed between leaves in the citrus canopy, and recently-hatched neonate larvae drop to the soil and feed on roots. The coccinellid species, *Cycloneda sanguinea* (L.), *Harmonia axyridis* Pallas, and *Olla v-nigrum* Mulsant, are generalist predators that consume a wide range of citrus pests, although they have not been observed preying on *Diaprepes*. We conducted experiments to determine whether these species would feed on *Diaprepes* egg masses and neonate larvae, and how an exclusive or partial diet of *Diaprepes* eggs would influence their development. The three predators responded very similarly in our tests. In laboratory assays, coccinellid larvae and adults readily consumed exposed *Diaprepes* eggs and neonates less than 48 h old; and coccinellid larvae preyed on 40% of intact egg masses laid between wax paper strips or citrus leaves, whereas adults preyed on 8.7%. In a greenhouse assay, coccinellid larvae located and preyed on 22.7% of intact egg masses laid between leaves on potted citrus trees. Although neonates might have relatively limited exposure to predation in the canopy before they drop to the soil, predation could be an important factor selecting for the timing of egg hatch, neonate escape from leaf envelopes, and neonate drop. The developmental assays indicate that *Diaprepes* eggs are less suitable prey for these coccinellid species than eggs of the flour moth, *Ephestia kuhniella* Zeller, but that they could be a highly acceptable component of a mixed diet. Our experiments indicate that these coccinellid species are potentially important predators of *Diaprepes* but the extent to which they contribute to the natural biological control of this weevil remains unknown.

Key Words: predation, development, biological control, integrated pest management, Curculionidae, Coccinellidae, *Cycloneda sanguinea*, *Harmonia axyridis*, *Olla v-nigrum*

RESUMEN

El picudo de los cítricos, *Diaprepes abbreviatus* (L.) es una plaga séria de cítricos en Florida. Hembras adultas ponen huevecillos en masas selladas dentro hojas en la copa del arbol, y las larvas neonatas recien-eclosionadas caen al suelo y comen de los raices. Las catarinitas *Cycloneda sanguinea* (L.), *Harmonia axyridis* Pallas, and *Olla v-nigrum* Mulsant son depredadores generalistas que consumen un rango amplio de insectos dañinos en citricultura, aunque no han sido observados consumiendo *Diaprepes*. Experimentos fueron llevado a cabo para determinar si estas espécies consumiera huevos y neonatos de *Diaprepes*, y como dietas de huevecillos y neonatos, exclusivas o parciales, influiera su desarollo larval. Los tres depredadores respondieron en forma parecida en nuestros experimentos. In pruebas de laboratório, larvas y adultos consumieron en seguida huevecillos de *Diaprepes* expuestos y neonatos menos que 48 h de edad. Larvas atacaron 40% de masas de huevecillos sellado dentro hojas de papel encerado, o hojas de citrus, mientras que adultos atacaron 8.7%. En una prueba de invernadero, larvas de Coccinellidae atacaron 22.7% de masas de huevecillos en arboles de cítricos en tiestos. Aunque los neonatos no son exquesto a la depredacion por largo plazo en el arbol antes de caer al suelo, la depredacion puede ser un factor importante en la evolución del tiempo de eclosión de huevecillos, salida de neonatos del sobre de hojas, y caida de neonatos al suelo. Las pruebas de desarollo mostraron que los huevecillos de *Diaprepes* son presas menos apropiadas para larvas de estas espécies que huevecillos del pomilla de harina, *Ephestia kuhniella* Zeller, pero indican que huevecillos de *Diaprepes* podian ser una presa altamente acceptable dentro una dieta mesclada. Sobre todo, nuestros experimentos indican que éstas espécies de Coccinellidae son depredadores de *Diaprepes* potencialmente importante, pero el alcance de tal depredacion en la naturaleza queda desconocido.

Translation provided by author.

The root weevil, *Diaprepes abbreviatus* (L.), apparently originated in the Caribbean and is now a major introduced pest of citrus, sugar cane, and or-namentals in Florida (Simpson et al. 1996). In citrus, larval feeding damages roots, reduces yield, and kills trees by girdling or by facilitating infec-

tion by plant pathogens such as *Phytophthora* spp. (Graham et al. 1996). The combination of *Diaprepes* and *Phytophthora* can lead to rapid tree decline and destroy groves within a few years of a weevil infestation. Adults are long lived and feed on foliage, especially new growth. Mating occurs in the canopy, and eggs are laid in masses between leaves that are glued together by an adhesive secreted by the female during oviposition. The larvae hatch, escape from the sealed leaf envelope, drop to the soil, and burrow down to the roots where they begin feeding. As they grow, the larvae move to larger roots, and pupate in the soil after 9-11 instars (Woodruff 1985; Quintela et al. 1998; McCoy 1999).

Sources of mortality for the various life stages of *Diaprepes* include numerous predators and parasites. Several egg parasitoids have been discovered in the Caribbean and introduced into Florida for biological control (Hall et al. 2001). Eggs are also subject to predation by ants, crickets, earwigs, lacewings, and spiders. Newly-hatched neonate larvae are especially prone to predation on the soil surface where they are attacked by ants, earwigs, hemipterans, and spiders whereas larvae below ground are attacked by ants and entomopathogenic nematodes. Adults are preyed on by ants, birds, lizards, snakes and spiders (Whitcomb et al. 1982; Richman et al. 1983a,b; Tryon 1986; Jaffe et al. 1990; McCoy et al. 2000; Stuart et al. in press).

In developing an effective IPM program to control *D. abbreviatus*, it would be advantageous to maximize the effectiveness of as many of the natural enemies of this insect as possible. Several coccinellid species including *Cycloneda sanguinea* (L.), *Harmonia axyridis* Pallas, and *Olla v-nigrum* Mulsant, are common in Florida citrus groves where they prey primarily on various aphid species (Michaud 2000). Although these coccinellids have not been reported preying on *Diaprepes*, coccinellids are known to consume a wide range of prey including certain weevil larvae (Kalaskar & Evans 2001). Moreover, these coccinellid species coexist with *Diaprepes* in the citrus canopy and are likely to encounter *Diaprepes* egg masses and possibly neonate larvae, before the larvae escape from their sealed leaf envelopes and drop to the soil. Hence, coccinellids might contribute to the natural biological control of this weevil, and we conducted laboratory experiments to determine whether these species could be effective predators on *Diaprepes* egg masses and neonates. We also conducted experiments to determine how an exclusive or partial diet of *Diaprepes* eggs would influence the development of these species.

MATERIALS AND METHODS

Rearing

Laboratory colonies of *Harmonia axyridis*, *Cycloneda sanguinea*, and *Olla v-nigrum* were reared on frozen eggs of the flour moth, *Ephestia kuhniella* Zeller, and bee pollen as described by Michaud (in press). Coccinellid eggs were collected from ovipositing females and incubated as described by Michaud (2000) to produce larvae used in experiments. *Diaprepes abbreviatus* eggs were obtained from laboratory colonies where they were laid between strips of wax paper or between citrus leaves. Leaves that were presented to weevils for oviposition were held together with paper clips, and the leaf petioles were wrapped with wet cotton and parafilm to prevent desiccation. *Diaprepes* neonates were obtained from egg masses laid between wax paper strips and were used in experiments within 48 h of their emergence from sealed egg masses. *Aphis gossypii* Glover were reared on cotton plants (*Gossypium hirsutum*, var. "SureGrow") in growth chambers at 20 ± 1°C, 16:8 L:D h, 60-65% RH. Laboratory experiments were conducted in plastic Petri dishes (5.5 cm dia × 1.0 cm) on open laboratory benches at 24 ± 1°C under fluorescent lights unless otherwise noted.

Prey Acceptability

Tests were performed to determine the relative acceptability of *Diaprepes* eggs and neonates as prey for larvae and adults of the three coccinellid species. In the first test, individual first-instar coccinellid larvae (<24 h old) were transferred to plastic Petri dishes (as above) containing an excess of *E. kuhniella* eggs (~0.1 gm) and a small *D. abbreviatus* egg mass of 10-19 eggs, which had been exposed by separating the wax paper strips between which the mass had been laid. We conducted 24-25 replicates per species, and the number of *D. abbreviatus* eggs consumed was recorded after 24 h. In the second test, 4-5 wk old adult coccinellids were similarly presented with excess *E. kuhniella* eggs and an exposed *Diaprepes* egg mass. We conducted 20 replicates per species, and predation was assessed after 24 h. In the third test, coccinellid larvae reared on *E. kuhniella* eggs to the third instar were presented with an excess of moth eggs and 10 *D. abbreviatus* neonates less than 48 h old. We conducted 18-20 replicates per species, and the number of *D. abbreviatus* larvae consumed was recorded after 24 h. In the fourth test, individual coccinellid adults were starved for 16 h and then transferred to plastic Petri dishes that contained 10 *A. gossypii* (a mixture of 4th instars and apterous adults) and 10 *D. abbreviatus* neonates. We conducted 13-16 replicates per species, and the numbers of *A. gossypii* and *D. abbreviatus* larvae consumed were recorded after 30 min.

Prey Accessibility

Laboratory tests were conducted to determine whether coccinellid larvae and adults could access

and prey upon intact *D. abbreviatus* egg masses that had been oviposited between strips of wax paper or between citrus leaves. The first test consisted of 18-20 replicates per species in which individual first instar coccinellid larvae that had been fed *E. kuhniella* eggs for 24-48 h post eclosion were transferred to a plastic Petri dish containing a *D. abbreviatus* egg mass laid between wax paper strips. After 24 h, the wax paper strips were pulled apart and predation assessed. The second test consisted of 10-20 replicates per species and was similar to the first test except that the egg mass had been laid between citrus leaves. Predation was similarly assessed. The third test used the same methodology and consisted of 19-20 replicates per species in which 4–5 wk old adult coccinellids from stock colonies were presented with egg masses that had been laid between wax paper strips. Predation was similarly assessed. Egg masses laid between wax paper strips were 2-5 days old at the time of testing whereas those between leaves were less than 24 h old.

For the experiments, egg masses oviposited by the weevils between wax paper strips were prepared by trimming the paper around the masses so that they would fit into the assay dishes, and by folding up the edges of the wax paper slightly to provide entry for the coccinellids without damaging the egg masses themselves or the integrity of the adhesive applied by the egg-laying weevil. Excess leaf material around egg masses laid by weevils between citrus leaves was also trimmed so that they would fit into assay dishes, again without damaging the egg masses themselves or the integrity of the adhesive sealing them between the leaves. Some of the egg masses laid by *Diaprepes* females between citrus leaves appeared to be poorly sealed, such that the leaves readily separated, exposing the eggs. Only well-sealed egg masses were used in our experiments.

A greenhouse experiment was conducted to investigate the accessibility of egg masses to predation by coccinellid larvae of the three species under more natural conditions. Fifty *D. abbreviatus* adults of unknown age were caged on each of three 3-year old Volkamer lemon trees for 24 h. The *D. abbreviatus* adults and cages were then removed and 50 first instar coccinellid larvae (24-36 h old) of each species were released, one species per tree. Larvae were restricted to trees by an application of Tanglefoot® (The Tanglefoot Company, Grand Rapids, MI 40504) around the trunk. The larvae were removed after 24 h, *D. abbreviatus* egg masses located, and predation assessed.

Prey Suitability

Two developmental assays were performed to assess the suitability of *D. abbreviatus* eggs as food for *H. axyridis*, *C. sanguinea*, and *O. v-nigrum* larvae. In the first assay, we conducted 30-32 replicates per species in which individual coccinellid larvae (<24 h old) were transferred to plastic Petri dishes with water encapsulated in polymer beads (Entomos, LLC 4445 SW 35th Terrace, Suite 310, Gainesville, FL 32608), and approximately half were fed frozen *E. kuhniella* eggs (control diet) and the other half frozen *D. abbreviatus* eggs daily until pupation. Additional water beads were supplied every three days. Procedures for the second assay were identical to the first except that 36-39 larvae of each species were reared individually on the control diet for four days until they were late second or early third instar, whereupon approximately half were transferred to new dishes and fed *D. abbreviatus* eggs until pupation, whereas the other half continued receiving the control diet. Mortality, time to pupation, time to adult emergence, and adult dry weight were recorded for each replicate in each experiment.

Data Analysis

Statistical analysis used the SAS System for Windows, release 6.12 (SAS Institute, Inc. 1990). Count data were transformed prior to analysis using square root transformations. Comparisons of means used PROC ANOVA, PROC GLM, and PROC TTEST. Comparisons of proportions were conducted using contingency table analysis and chi-square tests or Fisher's exact tests using PROC FREQ. Untransformed data are reported in tables and figures as means and standard errors. Differences were considered significant at the $P = 0.05$ level, but sequential Bonferroni adjustments of critical values were used as indicated below to maintain error rates at the stated values when multiple comparisons were made within experiments (Rice 1989).

RESULTS

Prey Acceptability

In the first choice test in which first instar coccinellid larvae were offered exposed *Diaprepes* eggs and an excess of wax moth eggs, *C. sanguinea* consumed *Diaprepes* eggs in 15 of 24 replicates, *H. axyridis* in 15 of 24 replicates, and *O. v-nigrum* in 13 of 25 replicates. There was no significant difference among coccinellid species in the proportion of replicates in which weevil eggs were consumed ($\chi^2 = 0.749$, $df = 2$, $P = 0.688$). Similarly, there was no significant difference among beetle species in the number of weevil eggs that were consumed (ANOVA, F = 1.610, $df = 2, 70$, $P = 0.2074$; Fig. 1).

In the second choice test in which coccinellid adults were offered exposed *Diaprepes* egg masses and an excess of moth eggs, adults of each of the three species consumed *Diaprepes* eggs in
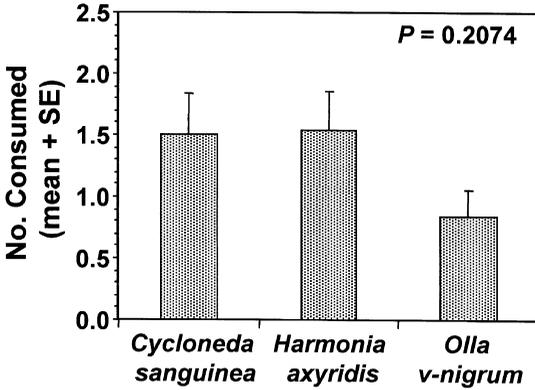
Fig. 1. Comparison of the number of *Diaprepes* eggs consumed by first instar coccinellid larvae when offered 10-19 *D. abbreviatus* eggs and an excess of flour moth eggs. The *P*-value is from an ANOVA (see text).

19 of 20 replicates. The number of eggs consumed was not recorded. In the third choice test in which third instar coccinellid larvae were offered 10 *D. abbreviatus* neonates and an excess of moth eggs, all three species ate at least some *Diaprepes* neonates in all replicates, and there was no significant difference in the number of neonates consumed among coccinellid species (ANOVA, F = 0.10, *df* = 2, 55, *P* = 0.9055; Fig. 2). In the fourth choice test in which coccinellid adults were offered 10 *A. gossypii* and 10 *D. abbreviatus* larvae, all three species ate more *Diaprepes* larvae than aphids (Fig. 3). Based on ANOVA, the main effect for coccinellid species was significant (F = 4.60, *df* = 2, 82, *P* = 0.128) with *O. v-nigrum* consuming less than the other two species, which did not differ. The main effect for prey species was also sig-

Fig. 3. Comparison of the number of *Diaprepes* neonates versus the number of *A. gossypii* consumed by adults of the three coccinellid species. ANOVA indicates that more *Diaprepes* were consumed than aphids, that *O. v-nigrum* consumed less than the other two predator species, which did not differ, and that the interaction between predator species and prey species was not significant (see text).

nificant (F = 24.15, *df* = 1, 82, *P* = 0.0001) with more *Diaprepes* being consumed than aphids; and the interaction between predator species and prey species was not significant (F = 1.95, *df* = 2, 82, *P* = 0.1489). However, in this experiment the *Diaprepes* larvae tended to stay on the bottom of the dishes whereas the aphids often moved up the sides and onto the lids, and this differential distribution of prey types might have contributed to the different consumption rates.

Prey Accessibility

When *Diaprepes* egg masses oviposited between wax paper strips were offered to first instar coccinellid larvae, *C. sanguinea* successfully penetrated between the strips and preyed on eggs in 4 of 20 replicates, *H. axyridis* in 10 of 20 replicates, and *O. v-nigrum* in 7 of 18 replicates. For egg masses between citrus leaves, *C. sanguinea* larvae successfully penetrated between the leaves
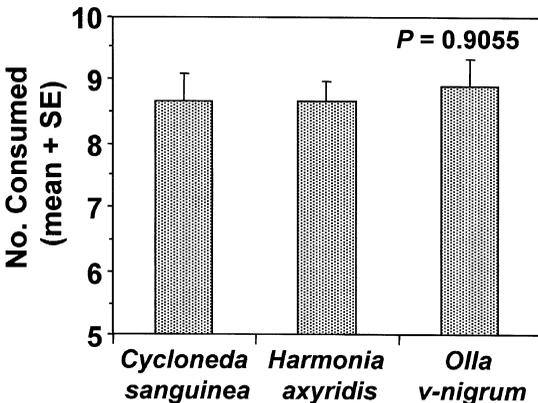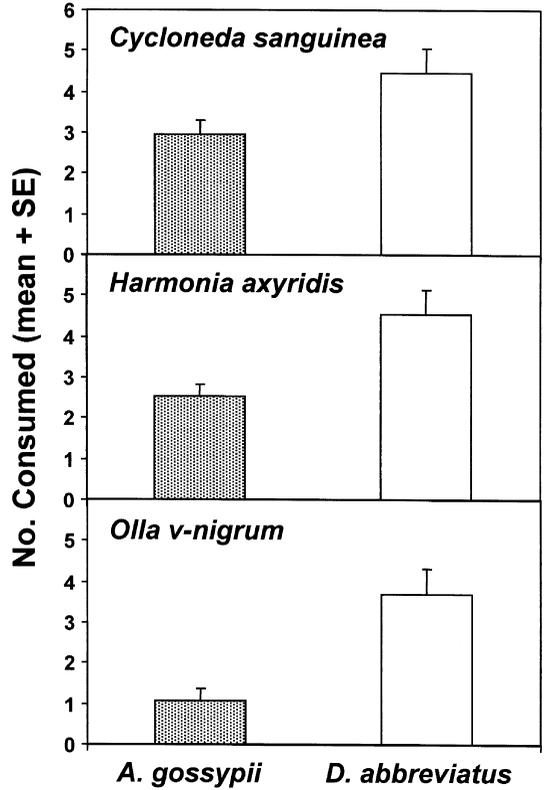

Fig. 2. Comparison of the number of *Diaprepes* neonates consumed by third instar larvae of the three coccinellid species when offered 10 neonates and an excess of flour moth eggs. The *P*-value is from an ANOVA (see text).

and preyed on eggs in 3 of 10 replicates, *H. axyridis* larvae in 7 of 19 replicates, and *O. v-nigrum* larvae in 12 of 20 replicates. There were no significant differences among coccinellid larvae of different species in the proportion of egg masses that were preyed upon for wax paper (2×3 contingency table, $\chi^2 = 3.978$, $df = 2$, $P = 0.137$), leaves (2×3 contingency table, $\chi^2 = 3.239$, $df = 2$, $P = 0.198$), or for both substrates pooled (2×3 contingency table, $\chi^2 = 5.255$, $df = 2$, $P = 0.072$). Also, pooling the data for larvae of all three predator species, there was no significant difference for wax paper versus citrus leaves in the proportion of egg masses that were preyed upon (2×2 contingency table, $\chi^2 = 0.835$, $df = 1$, $P = 0.361$). Coccinellid larvae successfully preyed on 36.2% of egg masses sealed in wax paper, 44.9% sealed between citrus leaves, and 40.2% overall.

When coccinellid adults were offered egg masses sealed between wax paper strips, *C. sanguinea* penetrated between the strips and preyed on eggs in 0 of 20 replicates, *H. axyridis* in 1 of 20 replicates, and *O. v-nigrum* in 4 of 19 replicates, for an overall success rate of 8.5%. The largest difference in this experiment, that between *C. sanguinea* and *O. v-nigrum*, was borderline significant (Fisher's exact test, $P = 0.047$), but this result was rendered nonsignificant when sequential Bonferroni adjustments of critical values were made with respect to the total number of comparisons within the experiment (n = 3; Rice 1989). Therefore, again, no significant difference among beetle species was evident.

In the greenhouse experiment, relatively few egg masses were laid on the lemon trees but first instar larvae of all three coccinellid species successfully preyed on some of them. *C. sanguinea* preyed on 1 of 5 egg masses, *H. axyridis* on 2 of 10 egg masses, and *O. v-nigrum* on 2 of 7 egg masses, for an overall predation rate of 22.7%. None of the differences among predator species in this experiment was significant (Fisher's exact tests, P > 0.05). Thus, larvae of all three coccinellid species were capable of locating, accessing, and preying upon *Diaprepes* egg masses.

Prey Suitability

Coccinellids reared on *Diaprepes* eggs generally did worse than those reared on flour moth eggs. Significantly fewer larvae of each coccinellid species survived to adulthood when reared on an exclusive diet of *Diaprepes* eggs than when fed moth eggs, adult dry weight was significantly reduced, and developmental time was significantly extended (Table 1). Coccinellid larvae of each species reared on *Diaprepes* eggs from the third instar onward survived to become adults as well as those reared entirely on flour moth eggs, but adult weight was still significantly lower and development time significantly longer (Table 1).

DISCUSSION

This study demonstrates that coccinellid larvae and adults are potentially important predators of *Diaprepes abbreviatus* eggs and neonate larvae. The frequent consumption of *Diaprepes* eggs and neonates by coccinellid larvae and adults in these time-limited laboratory tests when other acceptable food was present and abundant indicates that these prey items are readily accepted by these predators. Moreover, young coccinellid larvae were especially capable of accessing and preying upon *Diaprepes* egg masses laid between wax paper strips or citrus leaves; and coccinellid adults exhibited this ability to a lesser extent. *Diaprepes* neonates drop to the soil soon after hatching (Woodruff 1985; McCoy 1999) and might have limited exposure to coccinellid predation in the canopy but predation pressure from coccinellids and other species could be an important factor selecting for the timing of egg hatch, neonate escape from leaf envelopes, and neonate drop.

The assays in this study provide little indication of differences among the three coccinellid species that might suggest that one is a more effective predator of *Diaprepes* eggs or neonates than the others. Only one of the experiments on prey acceptability, experiment 4, revealed any species differences. In this experiment, coccinellid adults were offered a choice between aphids and *Diaprepes* neonates, and *O. v-nigrum* ate less of both prey items than the other two species, which did not differ. No differences in prey accessibility or suitability were detected. Similar experiments with larger sample sizes might reveal differences, but the present data suggest that these would be minor. Potential differences among these species in terms of their foraging behavior in citrus groves or their relative abundances might make one species more effective than the others under field conditions.

The differential predation success exhibited by coccinellids in this study when presented with exposed eggs versus intact egg masses sealed between wax paper strips or citrus leaves indicated that egg masses laid between leaves are protected to some extent from predation by coccinellids. However, the success of some coccinellid larvae and adults in penetrating intact egg masses and preying on eggs indicates that this protection is far from absolute. Indeed, coccinellid larvae penetrated and preyed on sealed egg masses in over 40% of replicates whereas coccinellid adults did so in 8.5%. The penetration of intact egg masses by coccinellids suggests that these predators are responding to chemical cues associated with egg masses. Similar responses have been documented for coccinellids toward other prey (Obata 1986; Hattingh & Samways 1995).

Jaffe et al. (1990) noted that first instar *Diaprepes* larvae were somewhat repellent to various

TABLE 1. COMPARISONS OF THE RESULTS OF THE DEVELOPMENTAL ASSAYS IN WHICH THE THREE COCCINELLID SPECIES WERE REARED FOR EITHER THEIR ENTIRE DEVELOPMENT OR FROM THE THIRD INSTAR ONWARD ON A DIET OF EITHER *DIAPREPES* EGGS OR FLOUR MOTH EGGS.

Complete development	Flour moth eggs		*Diaprepes* eggs		
Survival	n	%	n	%	Statistical comparison
Cycloneda	16	68.8	15	13.3	χ^2 = 44.771, df = 1, P < 0.001
Harmonia	16	100.0	14	42.9	χ^2 = 32.604, df = 1, P < 0.001
Olla	16	100.0	16	37.5	χ^2 = 39.062, df = 1, P < 0.001
Adult weight (g)	Mean	SE	Mean	SE	
Cycloneda	3.1	0.15	1.6	0.45	F = 16.268, df = 1, 11, P = 0.002
Harmonia	9.9	0.31	5.1	0.45	F = 71.468, df = 1, 20, P < 0.001
Olla	6.0	0.19	3.0	0.30	F = 44.771, df = 1, 20, P < 0.001
Development time (d)	Mean	SE	Mean	SE	
Cycloneda	9.8	0.64	20.0	1.40	F = 58.259, df = 1, 14, P < 0.001
Harmonia	9.3	0.17	20.0	0.52	F = 672.364, df = 1, 20, P < 0.001
Olla	8.1	0.11	14.1	0.51	F = 274.067, df = 1, 21, P < 0.001
Development from 3rd instar					
Survival	n	%	n	%	
Cycloneda	18	100.0	18	83.3	χ^2 = 2.789, df = 1, ns
Harmonia	18	100.0	20	85.0	χ^2 = 2.250, df = 1, ns
Olla	19	94.7	20	80.0	χ^2 = 2.282, df = 1, ns
Adult weight (g)	Mean	SE	Mean	SE	
Cycloneda	3.9	0.14	2.1	0.12	F = 91.546, df = 1, 31, P < 0.001
Harmonia	10.8	1.31	6.1	0.18	F = 185.236, df = 1, 33, P < 0.001
Olla	6.2	0.21	2.9	0.11	F = 185.184, df = 1, 32, P < 0.001
Development time (d)	Mean	SE	Mean	SE	
Cycloneda	9.9	0.36	11.5	0.35	F = 9.513, df = 1, 32, P = 0.04
Harmonia	10.8	0.10	14.1	0.28	F = 94.119, df = 1, 33, P < 0.001
Olla	8.2	0.09	10.1	0.31	F = 39.601, df = 1, 32, P < 0.001

ant predators and that eggs less than 48 h old were often ignored by ants. Pavis et al. (1992) extracted and identified the chemicals apparently responsible for the repellency of the larvae and provided further evidence for their role in larval defense. Repellency of *Diaprepes* larvae to coccinellids was not observed in this study and was not evident in the experimental results. Moreover, as indicated by our leaf and greenhouse experiments, eggs less than 48 h old were not ignored by these predators. Thus, the chemical defenses of the larvae and apparent defenses of the eggs might only be applicable to certain taxa of predators. Defenses targeted toward ants would seem especially appropriate since ants are evidently the primary predators of various life stages of *Diaprepes* including egg masses and neonate larvae (Whitcomb et al. 1982; Richman et al. 1983a,b; Tryon 1986; Jaffe et al. 1990; McCoy 1999; Stuart et al. 2001). Deterrence of

coccinellids from attacking alfalfa weevil larvae has been attributed to the defensive wriggling of the larvae (Kalaskar & Evans 2001) but it is unclear whether wriggling might contribute to defense for *Diaprepes* larvae or whether alfalfa weevil larvae also possess chemical defenses.

Seasonal cycles of coccinellid and *Diaprepes* abundance in Florida citrus indicate considerable periods of overlap when predation is likely to occur. The three coccinellid species are present in groves year-round but are most abundant during periods of flowering and flushing, especially spring and fall. Flowers are attractive as sources of pollen and nectar for all three species, and most of their primary homopteran prey species require newly expanding leaves for their growth and reproduction. Hot weather in summer is typically associated with low food availability and a majority of individuals of all three species aestivate during these periods (Michaud, unpublished). In

central Florida, *Diaprepes* adults emerge in the spring and generally show a sharp peak in abundance sometime from April through June. However, emergence continues throughout the summer, and adults can remain abundant through mid November (McCoy, unpublished). Egg-laying occurs throughout this period, and neonate drop has been recorded from early July through early December (Nigg et al. in press). *Diaprepes* adults feed voraciously on newly-expanding leaves but lay egg masses between mature leaves (Woodruff 1985; McCoy 1999). Given their seasonal activity patterns and locations in trees, it is likely that coccinellids have frequent opportunities to prey on *D. abbreviatus* egg masses and perhaps on neonates as well.

The timing of *Diaprepes* egg hatch, neonate escape from sealed leaf envelopes, and neonate drop to the soil surface could have an important impact on the exposure of neonates to various predators. Jones & Schroeder (1983) found that a considerable period often elapsed between egg hatch and neonate escape from sealed leaf envelopes, estimated average larval age at the time of neonate drop to be about 48 h, and found that neonates dropped between 1100 and 2400 h. According to Richman et al. (1983), ant foraging on the soil surface during this time period is relatively low compared to early morning hours. Thus, the timing of neonate drop could be an adaptation to avoid peak ant foraging periods. The diurnal activity patterns of coccinellids in Florida citrus groves have not been studied but these species appear most active during daylight hours (Michaud, unpublished), and neonate drop late in the day might also enable avoidance of these predators. However, since *Diaprepes* neonates appear to remain within sealed leaf envelopes for relatively lengthy periods, there is a strong possibility that coccinellids will encounter neonates rather than eggs when penetrating leaf envelopes. Additional research on the activity patterns of predators, the factors that stimulate egg hatch and neonate drop, and the conditions that promote neonate survival in the canopy, on the soil surface, and below ground is necessary for a more thorough understanding of how these factors might shape *D. abbreviatus* life history and survival strategies.

Overall, our predation and developmental assays suggest that *Diaprepes* eggs and neonates could be a frequent and highly acceptable component of a mixed diet for these coccinellid species in nature. *Diaprepes* eggs were less suitable prey for these species than flour moth eggs but the costs in terms of reduced adult weight and extended developmental time were relatively small for larvae reared on this diet from the third instar. Similar suboptimal developmental results have been obtained for various coccinellid species and some of the aphid species that they frequently consume as prey (Michaud 2000). Thus, the results of this study, especially for coccinellid larvae, indicate that *Diaprepes* egg masses and neonates will be preyed upon quite readily when encountered. However, the frequency of such encounters and the intensity of predation in nature remain unknown; and it is unclear to what extent coccinellids contribute to the natural biological control of this weevil.

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