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REPELLENCY**

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Source: Florida Entomologist, 86(1) : 61-72

Published By: Florida Entomological Society

URL: [https://doi.org/10.1653/0015-4040\(2003\)086\[0061:PONLOD\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2003)086[0061:PONLOD]2.0.CO;2)

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PREDATION ON NEONATE LARVAE OF
DIAPREPES ABBREVIATUS (COLEOPTERA: CURCULIONIDAE)
IN FLORIDA CITRUS: TESTING FOR DAILY PATTERNS OF
NEONATE DROP, ANT PREDATORS AND CHEMICAL REPELLENCY

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ABSTRACT

The root weevil, *Diaprepes abbreviatus* (L.), is a major pest of Florida citrus. When neonate larvae hatch from egg masses in the citrus canopy and drop to the soil surface before burrowing down to the roots for feeding, they are vulnerable to ant predation. However, neonates are reported to produce a chemical repellent that lasts up to four days and reduces ant predation by about 40%. We assessed the daily pattern of neonate drop from egg masses under laboratory conditions (24°C, 70% RH, L:D = 12:12), examined the role of ants as predators of neonates (<48 h post hatch) on the soil surface in three citrus groves in central Florida, and tested for chemical repellency in the field by comparing predation rates on 5-day versus 1-2 h old neonates. Neonate drop was not well synchronized within or among egg masses, occurred during all hours of the light and dark phases, and extended over 5 to 23 h (mean = 11.97, SE = 0.866) for individual egg masses (n = 29). However, the drop rate was highest during the second half of the light phase (52.4%) and lowest during the second half of the dark phase (8.0%). Predation occurred in 104 of 199 replicates (52.3%) in the three groves with a total of 475 of the 3980 larvae (11.9%) removed by predators within 20 mins. Predation pressure varied within and among groves, and involved eight ant species (Hymenoptera: Formicidae) and a single predation event by a nymph of the big-eyed bug, *Geocoris floridanus* Blatchley (Hemiptera: Lygaeidae). For data pooled among groves, the red imported fire ant, *Solenopsis invicta* Buren, was responsible for 29.5% of the predation, *Pheidole moerens* Wheeler 27.8%, *Dorymyrmex reginacula* (Trager) 9.7%, *Brachymyrmex obscurior* Forel 8.8%, *Dorymyrmex bureni* (Trager) 8.6%, *Cardiocondyla emeryi* Forel 8.0%, *Paratrechina bourbonica* Forel 4.8%, and *Pheidole morrisi* Forel 2.5%. In our test for age-dependent chemical repellency, a total of 2620 of the 3840 neonates (68.2%) were preyed upon within 30 mins but the predation rate on old versus young neonates did not differ at 68.8% and 67.7%, respectively. In this experiment, 368 of the predation events (14.0%) were observed directly with *P. moerens* responsible for 62.5%, *S. invicta* 25.3%, *C. emeryi* 10.1%, *B. obscurior* 1.4%, *Cardiocondyla wroughtonii* (Forel) 0.5%, and *D. bureni* 0.3%. We conclude that ants are important predators of *Diaprepes* neonates in central Florida citrus groves and have potential for a conservation biological control program.

Key Words: predation, ants, biological control, integrated pest management, red imported fire ant, Curculionidae, Formicidae

RESUMEN

El picudo de la raíz, *Diaprepes abbreviatus* (L.), es una plaga importante de cítricos en la Florida. Cuando las larvas neonatas (recién nacidas) esclosionan de las masas de huevos en la copa de los árboles de cítricos y caen a la superficie del suelo escavando hacia abajo en las raíces para alimentarse, ellas están vulnerables a la depredación por las hormigas. No obstante, se reportan que las neonatas producen un químico repelente que dura hasta cuatro días y reduce la depredación por las hormigas por aproximadamente 40%. Nosotros evaluamos el patrón diario de la caída de las neonatas de las masas de huevos bajo condiciones en el laboratorio (24°C, 70% RH, L:D = 12:12) [RH = Humedad Relativa; L:D = Luz:Oscuridad], examinamos el papel de las hormigas como depredadores de las neonatas (<48 h después de esclosionar) sobre la superficie del suelo en tres huertos de cítricos en central Florida, y probamos la habilidad del químico para repelar en el campo comparando las tasas de depredación sobre las neonatas de 5-días versus 1-2 horas de edad. La caída de las neonatas no fué bien sincronizada dentro de la misma o en diferentes masas de huevos, más ocurrió durante todas las horas de las fases de luz y oscuridad, y se extendió de 5 a 23 horas (promedio = 11.97, SE = 0.866) para las masas de huevos individuales (n = 29). No obstante, la tasa de la caída fué la más alta durante la segunda mitad de la fase de luz (52.4%) y la más baja durante la segunda mitad de la fase (8.0%). La depredación ocurrió en 104 de las 199 replicas (52.3%) en tres huertos con un total de 475 de los 3980 larvas (11.9%) eliminadas por los depredadores dentro de 20 minutos. La presión de los depredadores varió dentro del mismo y en dife-

rentes huertos, y abarcó ocho especies de hormigas (Hymenoptera: Formicidae) y un solo evento de depredación por parte de una ninfa del chinche de ojos grandes, *Geocoris floridanus* Blatchley (Hemiptera: Lygaeidae). Por los datos colectados entre todos los huertos, la hormiga de fuego importada, *Solenopsis invicta* Buren, fué responsable por el 29.5% de la depredación, *Pheidole moerens* Wheeler 27.8%, *Dorymyrmex reginica* (Trager) 9.7%, *Brachymyrmex obscurior* Forel 8.8%, *Dorymyrmex bureni* (Trager) 8.6%, *Cardiocondyla emeryi* Forel 8.0%, *Paratrechina bourbonica* Forel 4.8%, y *Pheidole morrisi* Forel 2.5%. En nuestra prueba de la repelencia químico dependiendo de la edad, un total de 2620 de los 3840 neonatas (68.2%) fueron atacadas dentro de 30 minutos pero la tasa de depredación sobre neonatas viejas versus neonatas juvenes no fué diferente siendo 68.8% y 67.7%, respectivamente. En este experimento, 368 de los eventos de depredación (14.0%) fueron observados directamente con *P. moerens* responsable por 62.5%, *S. invicta* 25.3%, *C. emeryi* 10.1%, *B. obscurior* 1.4%, *Cardiocondyla wroughtonii* (Forel) 0.5%, y *D. bureni* 0.3%. Nosotros concluimos que las hormigas son depredadores importantes de neonatas de *Diaprepes* en los huertos de cítricos en central Florida y tienen potencial en un programa de conservación de control biológico.

The root weevil, *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae), is a major pest of citrus, ornamentals, and other crops, and has spread widely in Florida since it was first detected in 1964 (Graham et al. 1996, McCoy 1999, McCoy et al. 2001). 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). In citrus, larval feeding reduces yield, girdles trees, and facilitates infections by plant pathogens such as *Phytophthora* spp. The combination of *Diaprepes* and *Phytophthora* can cause severe tree decline and destroy groves within a few years of an initial infestation (Graham et al. 1996). In developing an effective integrated pest management (IPM) program for *D. abbreviatus*, it is important to maximize the effectiveness of natural enemies. Preliminary research indicates that some of the major mortality agents of *Diaprepes* eggs, larvae, and adults are predators; and that the primary predators are ants (Whitcomb et al. 1982; Richman et al. 1983, Stuart et al. 2002, in press, Stuart & McCoy, in press).

Ants are recognized as important predators of pest insects in various agroecosystems and are subject to conservation in some IPM programs (Way & Khoo 1992, Perfecto & Castiñeiras 1998, Eubanks 2001). Indeed, the use of ants to control citrus pests in Asia dates back to at least 304 AD, is the earliest known example of biological control, and is still practiced today (Way & Khoo 1992). Florida has a rich and diverse ant fauna numbering over 200 species (Deyrup et al. 2000), and ants can be extremely abundant in Florida citrus groves (Whitcomb et al. 1982, Richman et al. 1983; Tryon 1986, Stuart & McCoy, in press, Stuart et al. in press). Under the proper condi-

tions and with appropriate management, ants could constitute a major weapon in our fight against *Diaprepes*, and a conservation biological control program focusing on appropriate ant species might well be the key to controlling this insect (Whitcomb et al. 1982, Jaffe et al. 1990, Stuart & McCoy, in press; Stuart et al. in press). However, at present, it is unclear which ant species are the most effective predators of *Diaprepes* on the soil surface, in the canopy, and below ground, and what strategies might be most effective in promoting and conserving beneficial ant species (Whitcomb et al. 1982, Richman et al. 1983, Stuart & McCoy, in press, Stuart et al. in press). Natural variability in the abundance and distribution of ants, combined with various possible influences of citrus management practices could contribute to considerable variability in predation pressure by ants on *Diaprepes* within and among groves across the state (e.g., see McCoy et al. 2001). Our present research begins to address these issues by assessing the role of ants as predators of *Diaprepes* neonate larvae on the soil surface in citrus groves in central Florida.

The timing of *Diaprepes* egg hatch, neonate escape from sealed leaf envelopes, and neonate drop to the soil surface could influence the relative exposure of neonates to predation (Whitcomb et al. 1982, Richman et al. 1983, Stuart et al. 2002). Jones & Schroeder (1983) found that a considerable period often elapsed between egg hatch and neonate escape from 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. Ant foraging on the soil surface during this period is reported to be low compared to early morning hours, and the timing of neonate drop could be an adaptation to avoid peak foraging periods (Whitcomb et al. 1982; Richman et al. 1983). Unfortunately, Jones & Schroeder (1983) examined neonate drop for only five egg masses, and did not report any information on the light cycles used in their laboratory experiments. 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 (Stuart et al. 2002).

Jaffe et al. (1990) observed that first instar *Diaprepes* larvae were preyed upon by various ant species but that the larvae appeared to be somewhat repellent, and Jaffe et al. suggested that the larvae might have chemical defenses. Pavis et al. (1992) investigated this chemical repellency with respect to the fire ant, *Solenopsis geminata* (F.), on the island of Guadeloupe in the Caribbean and identified two bicyclic sesquiterpene aldehydes that appeared to be responsible for the effect. The concentration of the repellent was highest in newly-hatched neonates, decreased with larval age, and was absent after about four days. Pavis et al. (1992) suggested that ant predation on neonate larvae during the first few hours after hatching would be reduced by about 40% because of chemical repellency. Various coccinellid species readily consume *Diaprepes* neonates under laboratory conditions with no indication of repellency (Stuart et al. 2002), and no experimental demonstrations of neonate repellency against other ant species have yet been reported (Stuart & McCoy, in press).

Our objectives in the present study were to (i) assess the daily temporal pattern of neonate drop from *Diaprepes* egg masses under controlled laboratory conditions, (ii) evaluate predation pressure on neonates on the soil surface in a series of citrus groves in central Florida, and (iii) test for neonate age-dependent chemical repellency by comparing predation rates on neonates of different ages under field conditions in central Florida.

MATERIALS AND METHODS

Neonate Drop

Egg masses laid between wax paper strips were obtained from a *Diaprepes* colony that was maintained on citrus foliage in a greenhouse at the Citrus Research and Education Center, Lake Alfred, FL. Egg masses were transferred to environmental chambers (Gaffney Engineering, Gainesville, FL) at least 4-5 days prior to neonate drop and were held in glass funnels (6 cm dia.), each of which was placed over a moving clock face coated with Tanglefoot® (The Tanglefoot Company, Grand Rapids, MI, 40504). The clock face was fashioned from the lid of a plastic Petri dish (150 × 15 mm) on which 24 segments were marked to correspond to a 24-h clock. All one-hour segments will be referred to by the time at the beginning of the hour (e.g., the 0800 h one-hour time segment refers to the period from 0800 h to

0859 h). The clock face was secured to the top of the mechanical clock apparatus of a hygrothermograph (model H-302, Weather Measure Corporation, P.O. Box 41257, Sacramento, CA 95841). The top of the funnel was covered with the base of a small plastic Petri dish (60 × 15 mm) that was secured to the funnel with Parafilm® (American National Can, Menasha, WI 54952). Attached to the inside of the Petri dish was a vial of water sealed with a cotton plug to prevent the egg mass from drying out. The environmental chamber was set to 24°C, 70% RH, L:D = 12:12. Onset of the light phase was at 0800 h and of the dark phase was at 2000 h. We conducted 42 replicates during the period from 14 May through 28 October 2001, and each replicate involved a single egg mass. This included nine replicates that were conducted as controls in which the clock face was immobile to determine whether neonates would move between clock segments under these experimental conditions.

A two-way ANOVA (PROC GLM, SAS Institute Inc. 1990) with seven levels for the factor "date" and 24 levels for the factor "time" was conducted on the percent neonate drop from each egg mass after arcsin transformation. Means comparisons used the LSMEANS procedure (SAS Institute Inc. 1990). A similar ANOVA was conducted for the data pooled into four time intervals representing the first and second halves of the light and dark phases.

Predation

We conducted direct observations of predation on lab-reared *Diaprepes* neonates (<48 h post hatch) placed in citrus groves, and used procedures similar to those of Whitcomb et al. (1982) and Richman et al. (1983). Egg masses were obtained from a *Diaprepes* colony that was maintained on citrus foliage at the Citrus Research and Education Center, Lake Alfred, FL. Egg masses were held at room temperature in plastic containers that were arranged so that neonates hatching in the upper chamber could drop through a screen into the lower chamber. Neonates were removed from the lower chambers on a daily basis at 0800 h for use in experiments conducted that day. Each replicate consisted of 20 neonates placed in an open plastic dish (4 mm high × 48 mm dia, Millipore Petrislide containers, Millipore Corporation, Bedford, MA) on the soil surface under the canopy and observed for 20 min. A thin layer of fine sand that passed through a No. 40 sieve was placed in the bottom of the dish and effectively discouraged neonates from crawling out (see Richman et al. 1983), whereas roughening the outside and inside vertical surfaces of the dish with sand paper facilitated the entrance and exit of predators. A predation event was scored whenever a neonate was removed from the dish.

In most cases, predators were identified visually by field observers based on previously identified samples. In some cases, additional samples were taken to confirm identifications.

We conducted a total of 199 replicates in three groves located near the following municipalities in central Florida: Lake Alfred (63 replicates) and Alturas (58 replicates) in Polk County; and Southport (78 replicates) in Osceola County. In the Lake Alfred grove, which was located at the Citrus Research and Education Center of the University of Florida, we worked in two blocks, one of which was a mature planting of Marsh seedless grapefruit on Swingle citrumelo rootstock whereas the other was a close-set 5-year old planting of Navel orange on Swingle citrumelo rootstock. In the Southport grove, we worked in two mature blocks of Hamlin orange on Swingle citrumelo rootstock. The south block was being managed for commercial production whereas the north block had been abandoned because of severe tree decline, was no longer irrigated, and was subject to relatively little weed control. The Alturas grove was a uniform planting of mature Flame grapefruit on Swingle citrumelo rootstock and was under management for commercial production. Observations were conducted between 1 August and 11 September 2000, between 1200 and 1700 h. Minimum and maximum daily temperatures during this period at Lake Alfred, FL, ranged from 20.1 to 35.8°C.

Statistical comparisons of the proportion of replicates in which predation was observed and the proportion of neonates preyed upon in different groves and blocks were conducted using contingency table analyses and the χ^2 test (PROC FREQ, SAS Institute Inc. 1990).

Chemical Repellency

Twelve assay stations were established under the canopy of mature grapefruit trees (Marsh seedless grapefruit on Swingle citrumelo rootstock) with one station per tree at the Citrus Research and Education Center of the University of Florida, Lake Alfred, FL. *Diaprepes* egg masses laid between sheets of wax paper were obtained from the USDA rearing facility, Fort Pierce, FL. Egg masses were held as in the previous experiment; and neonates were harvested on a daily basis at 0800 h, and hourly on the day of the experiment. At each station, for each replicate, 20 neonates aged five days post hatching and 20 aged 1-2 h post hatching were placed in separate paired open plastic dishes (as described in the previous experiment), ca. 2-4 cm apart, on the soil surface near the trunk, for 30 min. The number of neonates remaining in the dishes was counted under a microscope at the termination of each replicate. Eight replicates were conducted, with the position of the dishes (i.e., left versus right) being randomized for the first replicate at each station,

and then alternated in successive replicates. Data were collected from six stations simultaneously, with stations 1-6 and 7-12 forming two distinct cohorts within the experiment, which were generally run sequentially. Direct observations of predation events, defined as a neonate being removed from an assay dish by a predator, were conducted during the experimental period for all replicates by systematically observing the dishes for 1-2 minute intervals as the test progressed. Observations were conducted during the period 21-26 July 2001, between 0850 and 1550 h. Weather data were recorded during the first 15 mins of each replicate by FAWN (Florida Automated Weather Network, University of Florida, Gainesville, FL) in an open field at the Citrus Research and Education Center, Lake Alfred, FL. These data include air temperature (measured 61.0 cm above the soil surface), soil temperature (measured 7.6 cm below the soil surface), relative humidity, and solar radiation.

A three-way ANOVA (PROC GLM, SAS Institute Inc. 1990) with two levels for the factor "age" (old and young), two levels for the factor "position" (left and right), and twelve levels for the factor "station" (1-12) was conducted on the percent predation in each dish after arcsin transformation. Means comparisons used the LSMEANS procedure (SAS Institute Inc. 1990). Percent predation on old versus young larvae by various ant species was compared using contingency table analysis and the χ^2 test (PROC FREQ, SAS Institute Inc. 1990).

RESULTS

Neonate Drop

The 42 egg masses contained from 21 to 127 eggs (total = 2687, mean = 63.98, SE = 3.983). A total of 491 eggs failed to hatch (18.3%), and an additional 60 eggs hatched but the neonates failed to exit the egg masses (2.2%). In two cases, the entire egg mass failed to hatch (4.8%). A total of 259 neonates dropped in the nine control replicates. Of these, 11 neonates moved across one clock-segment boundary (4.2%), and none moved across more than one boundary. In the 33 experimental replicates, less than 20 neonates dropped in four replicates, and only the remaining 29 replicates were considered in assessing the temporal pattern of neonate drop. In these 29 replicates, 23 to 125 neonates dropped per egg mass (total = 1865, mean = 64.31, SE = 5.410).

Neonates dropped during every hour of the light and dark phases, but there were significant differences in the percentage of neonates dropping among one-hour and six-hour time intervals (Fig. 1A, B). For the analysis involving 24 one-hour time intervals (Fig. 1A), the dates on which replicates were conducted had no influence on the

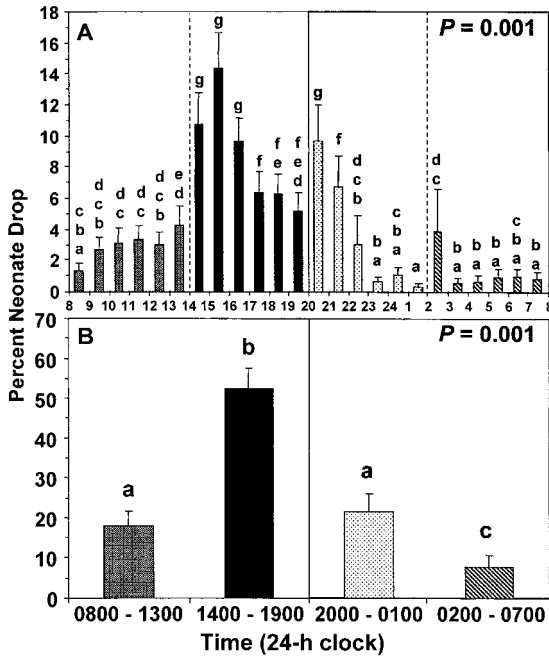


Fig. 1. Comparison of the percentage of neonates (mean + SE) that dropped from egg masses at various times of the day when the onset of the light phase was at 0800 h and the dark phase was at 2000 h with the data partitioned either hourly (A) or into six-hour time intervals (B). Statistical analysis was by way of ANOVA and LSMEANS. Common letters above bars indicate no significant difference at the $P = 0.05$ level.

results (ANOVA: $F = 1.01, df = 6, 528, P = 0.4148$) but time was a significant factor (ANOVA: $F = 12.50, df = 23, 528, P = 0.0001$) and the interaction between date and time was not significant (ANOVA: $F = 1.22, df = 138, 528, P = 0.0676$). Similarly, for the analysis involving four six-hour time intervals (Fig. 1B), the dates on which replicates were conducted had no influence on the results (ANOVA: $F = 0.13, df = 6, 88, P = 0.9928$) but time was a significant factor (ANOVA: $F = 22.32, df = 3, 88, P = 0.0001$) and the interaction between date and time was not significant (ANOVA: $F = 1.47, df = 18, 88, P = 0.1192$). On average, 17.9% of neonates dropped from 0800-1300 h, 52.4% from 1400-1900 h, 21.7% from 2000-0100 h, and 8.0% from 0200-0700 h.

The pattern of neonate drop for individual egg masses over the four six-hour time intervals defined above shows that the timing of neonate drop was not highly synchronized within or among egg masses (Fig. 2). For individual egg masses, neonates dropped over a period of 5 to 23 h (mean = 11.97, SE = 0.866). Of the 29 egg masses referred to above, 28 had neonates drop during both the light and dark phases (96.6%), 12 during all four of the six-hour time intervals (41.4%), 24 during at least three intervals (82.8%), 28 during at least

two intervals (96.6%), and one during only one interval (3.4%). All 29 egg masses had some neonates drop during the peak 6-h time interval from 1400-1900 h, 23 had more than 25% drop during this period (79.3%), 17 had more than 50% drop during this period (58.6%), and 8 had more than 75% drop during this period (27.6%). Two egg masses had more than 50% of their neonates drop from 0800-1300h (6.9%), three had more than 50% drop from 2000-0100 h (10.3%), and one had more than 50% drop from 0200-0700 h (3.4%).

Predation

We observed predation in 104 of 199 replicates (52.3%) with a total of 475 of the 3980 neonates being removed from assay dishes by predators (11.9%). All but one of the observed predation events were by ants (Hymenoptera: Formicidae). The single exception was by a nymph of the big-eyed bug, *Geocoris floridanus* Blatchley (Hemiptera: Lygaeidae), that attacked a neonate in the Lake Alfred grove. There was no significant difference in the proportion of replicates in which predation was observed at the three sites (Fig. 3A), but a greater proportion of neonates was preyed upon at the Alturas grove than at the other sites (Fig. 3B). Significant differences in the level of predation occurred within different areas of the groves. At the Lake Alfred grove, we observed no significant difference in the proportion of replicates that resulted in predation events in the grapefruit block versus the orange block (Fig. 3C), but a greater proportion of neonates was preyed upon in the orange block (Fig. 3D). At the Southport grove, we observed a highly significant difference in the proportion of replicates that resulted in predation events in the abandoned north block versus the cultivated south block (Fig. 3E), and a greater proportion of neonates was also preyed upon in the north block (Fig. 3F).

Eight ant species preyed on neonates in this experiment. For the data pooled from all sites, the red imported fire ant *Solenopsis invicta* Buren and *Pheidole moerens* Wheeler were the most active predators, and accounted for 29.5% and 27.8% of the predation events, respectively. Other predatory ant species in decreasing order of percent predation for the pooled data included *Dorymyrmex reginacula* (Trager) (9.7%), *Brachymyrmex obscurior* Forel (8.8%), *Dorymyrmex bureni* (Trager) (8.6%), *Cardiocondyla emeryi* Forel (8.0%), *Paratrechina bourbonica* Forel (4.8%), and *Pheidole morrisi* Forel (2.5%). Predation pressure by different ant species was variable within and among groves and probably reflects differences in the abundance and distribution of those species (Fig 4A, B). It is noteworthy that the Alturas grove was the site with the highest predation pressure on neonates (Fig. 3B) and was also the site in which *S. invicta* was the most active predator (Fig. 4A, B).

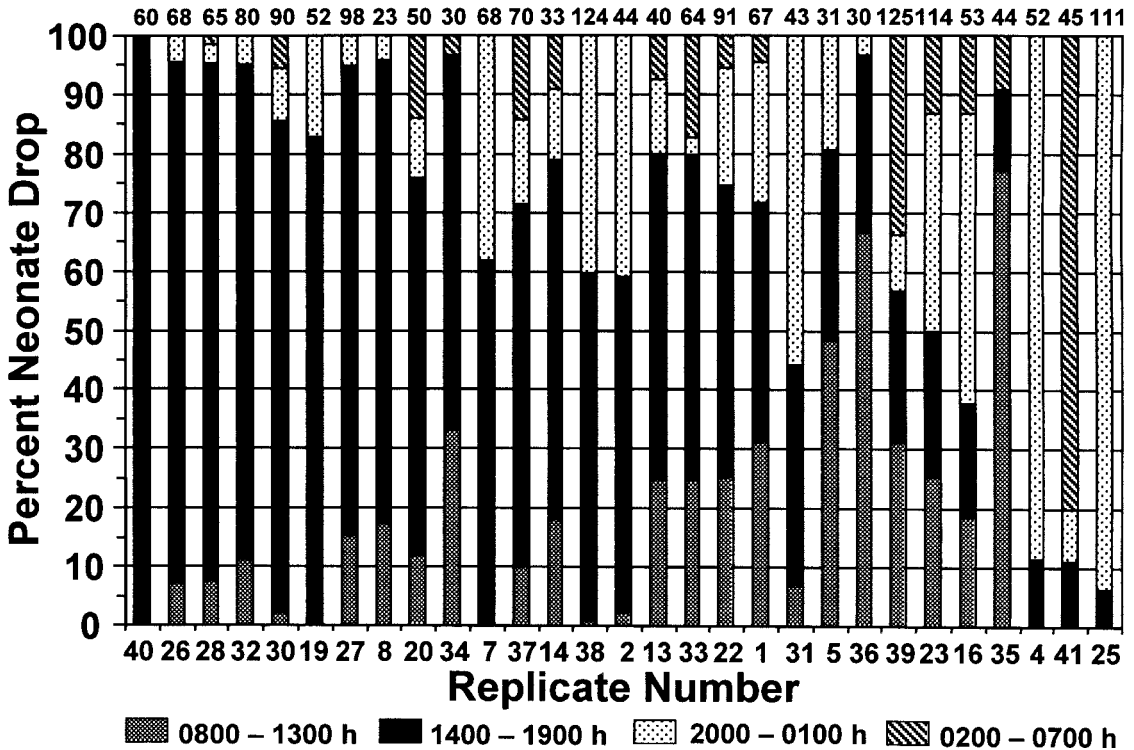


Fig. 2. Comparison of the percentage of neonates that dropped from egg masses at various times of the day for data partitioned into six-hour time intervals and ranked from left to right in descending order of the percentage of neonates that dropped during the peak time interval, 1400-1900 h (see Fig. 1). The replicate number is indicated below each bar, and the number of neonates dropping from the egg mass in that replicate is indicated above the bar.

Casual observations of the behavior of the ants in this study indicate that workers of different species often respond quite differently to *Diaprepes* neonates. Workers of both *Dorymyrmex* species are relatively large and fast moving, and often failed to respond to neonates as they quickly passed through assay dishes. *S. invicta* workers are also relatively large but move more slowly, and responded to neonates more frequently. We also noted that *S. invicta* often appeared to sting neonates before carrying them out of the dish, and that sometimes *S. invicta* workers appeared to have difficulty removing their sting from the body of the neonate and would wander about the dish with the neonate attached to the tip of their abdomen by the sting. Workers of the smaller species (i.e., *P. moerens*, *B. obscurior*, and *C. emeryi*) appeared to detect and respond to neonates more readily than the larger species. However, *P. moerens* workers typically seized and carried off neonates almost immediately upon contact whereas *B. obscurior* was more hesitant, often picked up and dropped neonates repeatedly, and sometimes abandoned the assay dish without a neonate. This handling difficulty is reminiscent of some of the behavior observed by previous researchers and

might be indicative of repellency (Jaffe et al. 1990, Pavis et al. 1992). *C. emeryi* was intermediate to the other two small species in terms of its handling efficiency. We did not observe mass recruitment of nestmates to assay dishes by any ant species in this experiment. Rather, predation appeared to be conducted by individually foraging workers that discovered and carried off a neonate, and often returned repeatedly to an assay dish to prey on additional neonates.

Chemical Repellency

A total of 2620 of the 3840 larvae (68.2%) were preyed upon in this experiment but the predation rate on 5-day old versus 1-2 h old *Diaprepes* neonates showed no significant difference at 68.8% and 67.7%, respectively (ANOVA: $F = 0.44$, $df = 1$, 144 , $P = 0.5067$). Both station and position were significant factors (ANOVA: station, $F = 19.27$, $df = 11$, 144 , $P = 0.0001$; position, $F = 5.56$, $df = 1$, 144 , $P = 0.0197$), and there was a highly significant interaction between station and position (ANOVA: $F = 6.11$, $df = 11$, 144 , $P = 0.0001$). The position of the assay dishes, whether left or right, had a significant impact on the percent predation

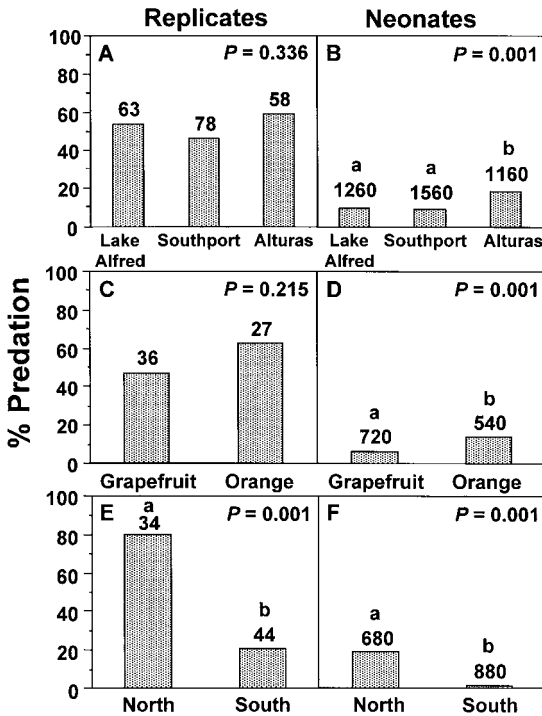


Fig. 3. Comparison of the percentage of replicates in which predation was observed (A, C, E) and the percentage of neonates preyed upon (B, D, F) in the three groves (A, B), and for different areas within two groves, Lake Alfred (C, D) and Southport (E, F). The numbers above the bars indicate the total number of replicates (A, C, E) or neonates (B, D, F). *P*-values indicate the results of χ^2 tests on 2×2 or 2×3 contingency tables. Common letters above bars indicate no significant difference at the *P* = 0.05 level. No letters appear above groups of bars where the overall contingency table analysis was not significant at the *P* = 0.05 level.

at five of the 12 stations, and predation was more intense at some stations than at others (Fig. 5A). At one station (#11), predation was 100% in both dishes in every replicate.

A total of 368 of the 2620 predation events (14.0%) were observed directly. All observed predation was by six ant species, with *P. moerens* and *S. invicta* preying on 62.5% and 25.3% of the neonates, respectively. Other ant species in decreasing order of percent predation included *C. emeryi* (10.1%), *B. obscurior* (1.4%), *Cardiocondyla wroughtonii* (Forel) (0.5%), and *D. bureni* (0.3%). *C. wroughtonii* was not observed as a predator in the previous experiment, and is the ninth predatory ant species reported here. The two predation events by *C. wroughtonii* occurred at the same assay station on successive days between 1520 and 1600 h. A comparison of the number of predation events by *P. moerens*, *S. invicta*, or the other ant species pooled on old versus young larvae revealed no significant differences (2×3 contin-

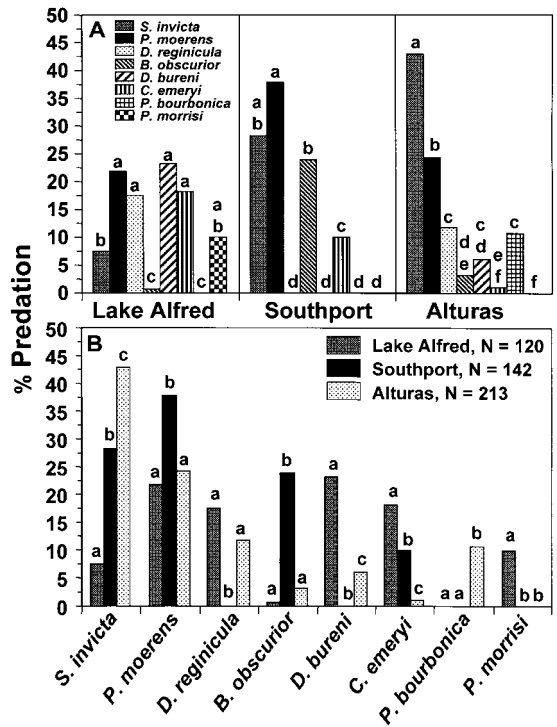


Fig. 4. Comparison of the percent predation by different ant species within and among the three groves. Statistical analysis was by way contingency tables and the χ^2 test. Common letters above bars indicate no significant difference at the *P* = 0.05 level either among species within sites (A) or within species among sites (B).

gency table, $\chi^2 = 4.170$, *df* = 2, *P* = 0.124; Fig. 5B). Thus, we found no evidence for age-dependent repellency of neonates, either overall or for particular ant species.

There was no correlation between time of day and percent predation for data pooled among stations and assay dish positions for stations 1-6 (Fig. 6A) but there was a significant increase in predation rate as the day progressed for stations 7-12 (Fig. 6B). There were no significant correlations between predation rate and air temperature, relative humidity, or solar radiation for either experimental cohort (Table 1). Soil temperature was correlated with predation rate for stations 7-12 but not for stations 1-6 (Table 1).

DISCUSSION

This study indicates that ants are important predators of *Diaprepes* neonates on the soil surface in the citrus groves of central Florida. Our laboratory data indicate that neonate larvae drop from the canopy during all hours of the day and night but that peak drop occurs during the afternoon. Our field tests demonstrate that at least nine ant species prey on neonates on the soil sur-

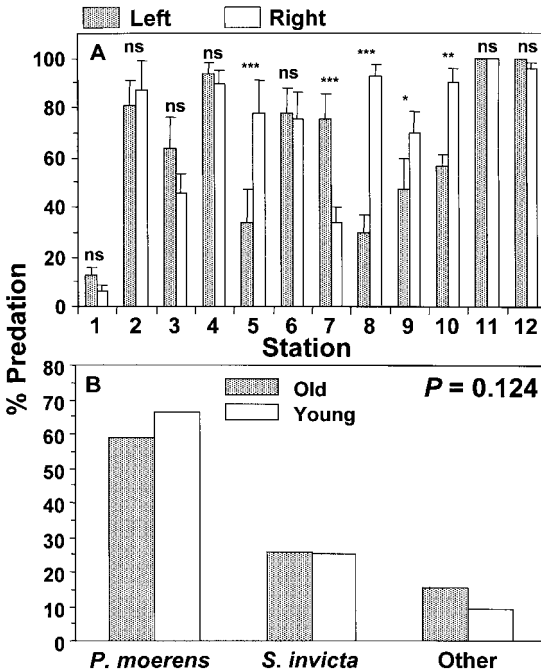


Fig. 5. Comparison of percent predation (mean + SE) on neonate larvae by ants for different assay-dish positions (left or right) at the 12 stations (A), and on old versus young neonate larvae by different ant species (B). Statistical analysis was by ANOVA and LSMEANS (A), or by contingency tables and the χ^2 test (B): ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

face, and are active during the peak drop period, but that predation pressure overall and by particular species can be highly variable within and among groves. Ants preying on *Diaprepes* neonates in this study included *Brachymyrmex obscurior*, *Cardiocondyla emeryi*, *C. wroughtonii*, *Dorymyrmex bureni*, *D. reginacula*, *Paratrechina bourbonica*, *Pheidole moerens*, *Ph. morrissi*, and *Solenopsis invicta*. A single predation event on a neonate by a nymph of the big-eyed bug, *Geocoris floridanus*, was also observed. We found no field evidence for differential predation on neonates of different ages by ants in this community and, hence, no evidence for age-dependent chemical repellency of neonates (see Jaffe et al. 1990, Pavis et al. 1992). However, behavioral observations indicate that ant species differ widely in their abilities to detect and handle this prey item and, consequently, the relative importance of particular species as predators of neonates is likely to depart markedly from their relative abundance in this agroecosystem. Our results reinforce the view that ants are among the primary mortality agents of *Diaprepes*, and have potential as the basis for a conservation biological control program (Whitcomb et al. 1982, Jaffe et al. 1990, Stuart & McCoy, in press, Stuart et al. in press).

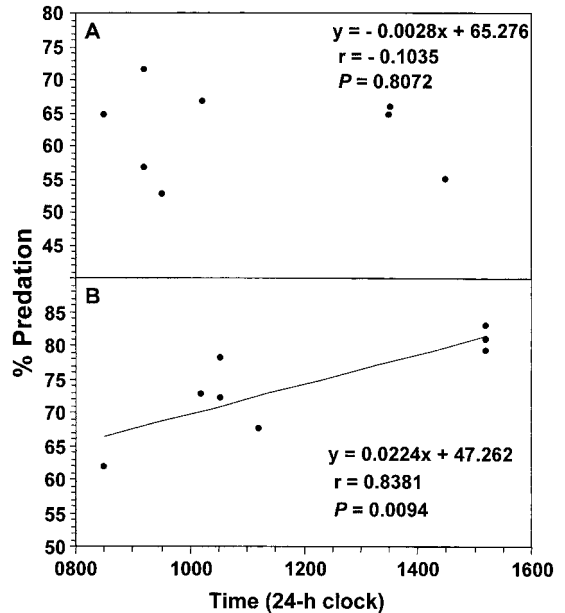


Fig. 6. Relationship between percent predation on neonate larvae and time of day for stations 1-6 (A) and 7-12 (B) of the chemical repellency experiment. The equation for the regression line, the Pearson correlation coefficient (r), and the P -value are given.

Previous research on ant predation on *Diaprepes* neonates in a central Florida citrus grove in Forest City, Seminole County, identified *Pheidole dentata* Mayr, *P. floridana* Emery, and *Tetramorium simillimum* Roger as the primary species involved (Whitcomb et al. 1982, Richman et al. 1983, Tryon 1986) but none of these species were detected in the present study. Moreover, whereas *S. invicta* and *P. moerens* were relatively minor predators in the previous studies, they were major predators in the present study. It is unclear whether this difference represents mere variability among sites or whether the ant fauna in central Florida citrus groves has undergone a dramatic change during this period. Florida has over 200 ant species, more than 50 of which are thought to be introduced, exotic species (Deyrup et al. 2000). Both *S. invicta* and *P. moerens* are exotic, and were classified by Deyrup et al. (2000) as "possible ecological villains" since they occur in both disturbed and undisturbed habitats, appear to dominate their trophic roles, and might displace native competitors. Indeed, both *S. invicta* and *P. moerens* appear to have spread "explosively" in Florida since they were first reported in 1950 and 1975, respectively (Deyrup et al. 2000). However, whereas *S. invicta* is considered a major invasive pest in a broad range of habitats and is often subject to intensive control efforts (see Vinson 1997), *P. moerens* has remained obscure (Deyrup et al. 2000). Notably, of the predatory ants

TABLE 1. SUMMARY AND CORRELATION ANALYSIS FOR THE PERCENT PREDATION AND WEATHER CONDITIONS IN EXPERIMENTS CONDUCTED AT STATIONS 1-6 AND 7-12 OF THE CHEMICAL REPELLENCY FIELD STUDY.

Station No.	Variable	N	Mean	SE	Range	Correlation with % Predation	
						R	P
1-6	Predation (%)	8	62.15	2.326	52.5-71.3	—	—
	Air Temperature (°C)	8	28.31	0.873	26.0-33.2	0.2660	0.5244
	Soil Temperature (°C)	8	28.61	0.462	26.9-31.1	-0.4654	0.2452
	Relative Humidity (%)	8	72.78	3.785	51.5-84.9	-0.3654	0.3734
	Solar Radiation (W/m ²)	8	416.14	87.233	61.0-722.0	0.2637	0.5281
7-12	Predation (%)	8	74.33	2.557	61.7-82.9	—	—
	Air Temperature (°C)	8	28.67	1.138	24.3-33.7	0.2842	0.4951
	Soil Temperature (°C)	8	28.76	0.370	27.2-30.6	0.7543	0.0306
	Relative Humidity (%)	8	72.04	4.905	52.0-90.7	-0.4979	0.2093
	Solar Radiation (W/m ²)	8	411.63	89.858	46.0-853.0	0.0287	0.9463

recorded in the present study, only the two *Dorymyrmex* species, *P. morrisoni*, and possibly *B. obscurior*, are considered native (Deyrup et al. 2000); and very little is known concerning the ecological dynamics of the highly synthetic ant community we now find in Florida citrus.

The results of the present study show how variable ant predation pressure on *Diaprepes* neonates can be in Florida citrus groves. Our experiments detected variation in predation rates among groves, among blocks within groves, among assay stations under a series of grapefruit trees, and between paired assay dishes only a few centimeters apart. This spatial variability probably reflects heterogeneity in the distribution and abundance of ant nests of various species. Unfortunately, there is little information on factors that might influence the distribution, growth, and activity levels of ant colonies of most species in this particular agroecosystem, but such information is necessary for the selective manipulation of species within a conservation biological control program. One exception is the red imported fire ant, *Solenopsis invicta*, since many aspects of its biology are well known (Vinson 1997). However, *S. invicta* is sometimes considered a citrus pest since it feeds on foliage and bark, can girdle young trees, tends aphids and scales, and disrupts harvesting by stinging grove workers (Banks et al. 1991, McCoy 1999, Michaud et al. 2002). Chemical suppression of *S. invicta* tends to increase ant diversity (McCoy et al. 2001) but, since *S. invicta* is such a voracious predator, it is unclear whether manipulating the ant community in this manner has a positive or a negative impact on the biological control of insect pests in general or of *Diaprepes* in particular. Whatever the case, *S. invicta* has become the dominant ant in many Florida citrus groves (Banks et al. 1991) and further studies of the positive and negative impacts of this and other ant species in this agroecosystem

seem warranted. In particular, we know virtually nothing about the biology of *P. moerens* (Deyrup et al. 2000) and its appearance as a major predator of *Diaprepes* neonates in the present study justifies further research.

Our results on the temporal pattern of neonate drop complement and extend those obtained previously. On the basis of five egg masses, Jones & Schroeder (1983) concluded that neonate drop occurred from 1100 to 2400 h but provided no further information on the temporal pattern observed, variability within or among egg masses, or on the light cycle under which these data were obtained. With a larger data set of 29 egg masses and controlled laboratory conditions (24°C, 70% RH, L:D = 12:12), we found that a peak in neonate drop occurred during the second half of the light phase but that neonate drop could occur during all hours of the light and dark phases, and that there was considerable variability in the timing of neonate drop within and among egg masses. In central Florida, neonate drop is closely associated with adult abundance and has been recorded from mid June to mid December (McCoy et al. in press, Nigg et al. in press). Further research is necessary to explore patterns of neonate drop under the range of light cycles and environmental conditions that occur during this period. At present, it is unclear what proximate or ultimate factors influence neonate drop, and to what extent temporal patterns are under genetic, developmental, or environmental control. Such patterns might constitute adaptive responses to the activity patterns of predators (Whitcomb et al. 1982, Richman et al. 1983, Stuart et al. 2002), or be influenced by environmental conditions such as rainfall, which could have an important impact on the ability of neonates to penetrate soil (Jones & Schroeder 1983).

Daily cycles in the foraging activity of ants in Florida citrus groves could be an important factor

regulating predation pressure on *Diaprepes* neonates. When Whitcomb et al. (1982) examined ant predation on neonates in a central Florida citrus grove using similar procedures to ours, they found no predation at 1200 h and 1500 h but 62%, 44% and 49% predation at 0700 h, 1800 h, and 2400 h, respectively. Richman et al. (1983) found predation levels of only 9.6% from 1200 to 1530 h in the same grove as the previous researchers but, since they used 50 neonates per dish rather than 20, their result might better be adjusted to 24.0% for a reasonable comparison. In the present experiments, we found a predation rate of 11.9% from 1200 to 1700 h when using a 20 min exposure period similar to those cited above, but a rate of 68.2% from 0850 to 1550 h when using a 30 min exposure period. Moreover, in the latter case, there was no evidence of a decline in predation rate during the day as suggested by the previous researchers. Indeed, in one cohort, there was a significant increase over the course of the day.

Current data suggest that ant foraging activity could be highly variable temporally and spatially in Florida citrus groves, and might depend more on the species involved, their relative abundance, and ambient environmental conditions than on time of day *per se*. According to Hölldobler & Wilson (1990), every ant species can be expected to have a distinctive foraging schedule. In some species, circadian rhythms have been demonstrated but can apparently be over-ridden or phase shifted by colony hunger, patterns of food availability, or other factors. To some extent, different foraging schedules among similar sympatric species might ultimately reflect coevolution and the temporal partitioning of resources, but could be based proximately on different humidity and temperature preferences or tolerances. However, in a detailed study of the foraging patterns of *Solenopsis invicta*, Porter & Tschinkel (1987) found that soil temperature, season, and rainfall explained most of the variation in foraging activity as indicated by food discoveries and recruitment to baits. Factors like time of day, even the difference between day and night, were not related to foraging activity. *S. invicta* foraged when soil temperatures at a depth of 2 cm ranged from 15 to 43°C, and exhibited maximum foraging rates between 22 and 36°C. Foraging was unusually low in late fall and was reduced during periods of rainfall. In the present research, we found that predation rates were related to time of day and soil temperature at some assay stations but not at others. Unfortunately, our weather records were based on measurements made in a nearby open field rather than under the citrus canopy where the experiments took place, and more detailed information regarding environmental conditions in this particular microhabitat might have been revealing. Further research is necessary to elucidate the foraging patterns of other ant spe-

cies in this community, the factors that regulate them, and how this might affect *Diaprepes* survival strategies.

This study indicates that there is no differential predation on 5-day versus 1-2 h old *Diaprepes* neonates by ants in a central Florida citrus grove. Thus, there is no evidence that a quantitative decrease in the chemical ant repellents produced by neonates over this time period as reported by Pavis et al. (1992) has any influence on the intensity of predation by this ant community. Our results are not necessarily in conflict with those of Pavis et al. (1992) since the repellents might be equally effective when present in small or large amounts, or might be totally ineffective against the ant species in this study, which did not include the species in their study, *Solenopsis geminata*. Furthermore, since Pavis et al. (1992) conducted their research on the island of Guadeloupe in the Caribbean, and since the *Diaprepes* population in Florida was introduced, perhaps as a few small founder populations (Bas et al. 2000), it is possible that the weevils in the two studies differ genetically and that the dynamics of the purported chemical ant-repellent system is different as well. Coccinellids are reported to be deterred from attacking alfalfa weevil larvae by their defensive wriggling (Kalaskar & Evans 2001), and it is unclear whether wriggling contributes to defense for *Diaprepes* larvae. Further research is necessary to explore these possibilities.

The predation assay used in the present study might underestimate predation pressure on *Diaprepes* neonates. This assay would miss any "sit and wait" predators (e.g., ant lions, various spiders) present under trees, and presents a novel substrate to mobile predators that might deter prey searching. It often appeared in our experiments that ants more readily walked around assay dishes than through them. However, these assay dishes might also facilitate predation by depriving neonates of cracks, crevices, and other complex elements of the leaf litter environment that might shelter them from predators or facilitate soil penetration. Jones & Schroeder (1983) found that the presence of grass stems and leaves placed vertically in soil did not promote soil penetration, and that neonates failed to penetrate dry soil. They also found that half of the groups of 20 neonates in their experiments that were aged 9 and 72 h required 80 and 105 mins, respectively, to penetrate below the surface of moist soil, and that all of the larvae in these groups disappeared below the surface within 180 mins. These results indicate that neonates might often remain on the soil surface for relatively long periods and that exposure times of 20 or 30 mins as used in our experiments are not excessive. Our experiments presented neonates to predators at an initial density of 20 neonates per assay dish, a density that would appear to constitute a relatively diffuse food resource and that

seems justified by the temporal pattern of neonate drop from individual egg masses observed in the present study. At this density, we found that ants discovering a neonate and carrying it off to their nest did not engage in the mass recruitment of nestmates but would often return to the assay dish repeatedly to prey on additional neonates, a foraging response common to many ant species and known as *Ortstreue* (Hölldobler & Wilson 1990). Neonates experimentally presented to predators at higher densities are reported to induce mass recruitment by some ant species (Whitcomb et al. 1982), and predation rates observed in such experiments might be considered artifacts of an unrealistically high neonate density. Consequently, we suggest low densities of the kind used here as a more realistic mode of neonate presentation for future experiments.

In general, the extent to which ants prey on various life stages of *Diaprepes* and are capable of controlling this insect will likely depend on the abundance and diversity of the ant species present. In turn, the structure of the ant community in particular citrus groves probably depends on an array of factors including local environmental conditions, grove management practices, and the dynamics associated with interactions among the various native and exotic species that become established within groves. Given the possible complexity of these factors and their interactions, it is premature to speculate upon what factors might have contributed to the variability in predation rates among groves and blocks within groves that we observed in the present study. Nonetheless, since ants are often extremely abundant in Florida citrus groves, and can be such important predators of a broad range of insect pests, considerable benefits could be derived from further studies of this ant community, the positive and negative impacts of different species, and how they might best be managed for pest control within the framework of a comprehensive IPM program. It might seem unusual to consider incorporating invasive exotic ant species into such a program but many of these species are now well established components of the ecological landscape in Florida and exploiting their beneficial aspects, especially in agricultural habitats, might be an extremely practical and cost-effective way of using these resources.

ACKNOWLEDGMENTS

We thank Angel Hoyte for rearing *Diaprepes* neonates, Karin Crosby for providing *Diaprepes* egg masses, Mark Deyrup for assistance with ant identification, Julieta Brambila for identifying the Hemipteran, and J. P. Michaud and H. N. Nigg for comments on the manuscript. This research was supported by the Florida Agricultural Experiment Station and a grant from the Florida Citrus Production Research Advisory Council, and approved for publication as Journal Series No. R-09033.

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