Reproductive Potential of Florida Populations of *Diaprepes abbreviatus* (Coleoptera: Curculionidae)[1]

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Abstract We examined the reproductive potential of field populations from five Florida geographical locations and one laboratory population of *Diaprepes abbreviatus* (L.). The life span for female weevils taken from field populations ranged from 116 to 300 d compared to 268 to 330 d for the laboratory population. Field-collected females oviposited a maximum of 11,414 eggs in 181 egg masses. The laboratory population produced a maximum of 20,048 eggs in 265 egg masses and may have been selected for egg production. The mean number of eggs, egg masses, and eggs/mass declined with female age for the laboratory-reared population. Compared to previous studies, our data increased the estimate of the maximum egg laying potential of individual females in field populations of *D. abbreviatus* from 7,000 to about 11,000 eggs. However, over a 6-wk period, the estimated life span for adults in the field, there was no difference in mean egg production between populations, and the overall mean ± S.E. was only 1954 ± 102 eggs (n = 184). Our data confirmed previous reports that females require fertilization by a male for egg development into a first-instar larva.

Key Words Oviposition, fecundity, field egg production

Diaprepes abbreviatus (L.) is an important pest for Florida and United States agriculture. Adult and larval stages feed on leaves, roots, or fruit of many agronomic and native host plants in Florida and several island nations of the Caribbean (Anonymous 1908, Jones 1915, Wolcott 1933, 1934, 1936, Fennah 1942, Woodruff 1968, Simpson et al. 1996). In the United States, agricultural host plants include citrus, corn, cotton, potatoes, tobacco, sugar cane, soybeans, and many ornamental plants (Simpson et al. 1996). There are approximately 66,420 ha in 21 Florida counties infested with this weevil (Hall 1995). *Diaprepes abbreviatus* has now been detected in California, Minnesota, and Texas. (S. E. Simpson, DOACS-DPI, pers. commun.).

Diaprepes abbreviatus is one of eight described species of root weevils in Florida and the largest known to infest citrus. Its larvae are of significant economic importance in both nursery and commercial citrus plantings due to the root injury caused by

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their feeding. Apparent visual plant damage resulting from adult *D. abbreviatus* is notching (feeding) of the margin of immature (not fully expanded) citrus leaves. It was initially thought that only young citrus trees could be seriously damaged by this weevil, but older trees are damaged and decline as a result of larval feeding on the tree roots (Griffith 1975).

Females oviposit eggs in a mass between two mature leaves held together with an adhesive (Adair et al. 1999) primarily between 10 p.m. and 6 a.m. (Schroeder 1981). After about 7 d, larvae hatch from the eggs and neonates fall to the soil surface beneath the host plant where they enter the soil to feed and develop. The larval period can last up to 1 yr with the development of eight instars (Wolcott 1933, 1934, Beavers 1982), but head capsule measurements suggest as many as 10 or 11 larval instars (Quintela et al. 1998). There may be a particularly inactive larval period (perhaps diapause) of 55 to 388 d before pupation (Wolcott 1936, Woodruff 1968). For pupation, a vertical chamber is formed in the soil where the larva compacts the soil. Pupation occurs within 15 to 20 d after the chamber is formed. Adult weevils emerge from the pupal case and spend a portion of their life in the soil (McCoy 1994). Wolcott (1936) found adults spent 11 to 126 d in the soil before emergence; most between 33 and 90 d. Adults emerge from the soil 6 mo to 2 yr after entering the soil as first-instar larvae (Griffith 1975). Adult abundance peaks in spring and, particularly, fall (McCoy et al. 2003, Nigg et al. 2003). More detailed studies of the pupation period of laboratory-reared *D. abbreviatus* as affected by soil moisture content (Lapointe and Shapiro 1999) and *D. abbreviatus* egg and larval development in the laboratory as affected by temperature (Lapointe 2000, 2001) have recently been published.

The reproductive potential of *D. abbreviatus* was first studied in the early 1900s (Jones 1915, Wolcott 1933, 1934, 1936). Wolcott (1936) reported a lifetime average of about 5,000 eggs for nine field-collected females from a Puerto Rican population. These females were held in the laboratory and fed citrus foliage (variety not stated). One female laid 7,046 eggs, six females laid about 5,000 eggs, and two females laid about 3,000 eggs during oviposition periods that ranged from 41 to 203 d (Wolcott 1936). The female depositing 7,046 eggs did so over 92 d (Wolcott 1936). Beavers (1982) collected field weevils, allowed the females to oviposit, and reared the emerging larvae to adults on an artificial diet. Twelve of these laboratory-reared, citrus-fed females were monitored for egg production and produced an average of 6,517 ± 931 eggs per female that had a mean ± S.E. longevity of 147 ± 17 d.

In a genetic relationship study of different Florida *D. abbreviatus* populations, we noted that 33 of 40 females from a Southport, FL, population failed to lay eggs when at 27 ± 1°C, 100% RH, and a photoperiod of 12:12 (L:D) h (Bas et al. 2000). This Southport population was distinct from five other populations by esterase staining, but grouped with three populations by RAPD-PCR (Bas et al. 2000). Southport weevils which laid eggs appeared to take a longer time between production of successive egg masses compared to five other Florida populations (Bas et al. 2000). This suggested to us that Florida *D. abbreviatus* populations might have different oviposition biologies. In addition, laboratory populations of any organism may become adapted to artificial rearing conditions, making aspects of their biology different from that of field populations (Prokopy and Economopoulos 1975, Leppla et al. 1976, Mazomenos et al. 1977, Leppla and Guy 1980, Styer and Greany 1983, Dipeolu 1984, Roush 1990a,b, Hooper et al. 1993).

The purpose of the present experiments was to assess the potential reproductive

capacity of five Florida field populations and one laboratory population of *D. abbreviatus.*

Materials and Methods

Populations. The same field population locations used in our previous genetic study (Bas et al. 2000) were used for this study. Our operational definition of a population is insects collected from a site about 50 ha in area. Sampled populations were separated by 35 to 394 km and were located near the following towns: Southport (near Poinciana, Osceola Co.), Lake Alfred (Polk Co.), Mt. Dora (Lake Co.), Vero Beach (Indian River Co.), and Homestead (Dade Co.). Field populations were collected based on availability (February through November; Futch 2002, McCoy et al. 2003), Southport (11 August 1998), Lake Alfred (30 September 1998), Mt. Dora (05 November 1998), Vero Beach population (04 December and 11 December 1998), Homestead population (22 February 1999). Field populations were collected by placing an umbrella under the foliage and beating with a dowel (Nigg et al. 1999). Captured weevils were placed in 5 cm round screen cages, transported within 4 h to the laboratory, and held as described below. The age and reproductive status of field individuals at the time of collection were not known.

The laboratory population was cultured at the USDA-ARS Horticultural Laboratory, Orlando, FL, now located at Ft. Pierce, FL, and was also the same source as our previous study (Bas et al. 2000). These weevils were shipped overnight as teneral, unmated adults. The Orlando laboratory population was from a colony established in 1975 from weevils captured in the Apopka, FL, area. Field weevils have been sporadically introduced into this colony from 1975 to 1997 (Lapointe 2000, 2001). Due to their rearing and holding conditions, the chronological age of adults when received varied from 30 to 90 d after emergence (K. Crosby, USDA, ARS, Ft. Pierce, FL, pers. comm.). Because all laboratory weevils were virgins when received, the "reproductive age" of females began with the receipt date as day 0. Laboratory #1 adults were received as teneral, virgin adults in individual containers and were held, males and females together, for 20 d before experimentation. All of these adults were assumed to have mated and to have become reproductive within the 20-d holding period. Laboratory #2 was received as teneral, virgin adults in individual containers on day 20 of the holding period for the laboratory #1, and were caged immediately as individual pairs for experimental purposes. All weevils regardless of source were held in the same insectary at 27 ± 1°C, 100% RH, and 12:12 (L:D) photoperiod.

Cages. Round 946-mL polypropylene containers with perforated plastic lids (Reynolds MVP, Mt. Vernon, KY, cup RD232, lid PL201) were prepared using one adult male and one adult female *D. abbreviatus* of the same population, a 2.5 × 0.5 cm cotton wick moistened with distilled, deionized water, a 2.5 cm × 25 cm wax paper egg-laying strip (Adair et al. 1999), and immature citrus leaves. Fresh immature citrus leaves and water were provided Mon, Wed, and Fri. Leaves were matched in area as they were picked so that all weevil pairs received the same quantity of foliage from the same source. Leaves were rinsed in glass-distilled, deionized water and then made into bouquets in a 30-mL plastic souffle cup with lid (Solo Cup Co., Urbana, IL, Lid No. PL1). The stem end of each leaf was inserted through a slit in the lid and immersed in glass-distilled, deionized water. Each bouquet contained 10 leaves so as to feed one pair of weevils *ad libitum* between food changes. Leaves were either from Kinkoji (*Citrus obovoidea* Hort. Ex Takahashi) seedlings or from Calamondin (× *Citroforton-*

ella microcarpa (Bunge) Wijnands) seedlings at each feeding. That is, the same variety was used for all weevils.

Seedlings were produced from certified seed from the Citrus Budwood Registration Bureau, Florida Department of Agriculture and Consumer Services, Winter Haven, FL. Seedlings were held in a glass house at 80 to 100% RH and 27 ± 2°C. No pesticides were applied to these plants. Plants were pruned routinely in order to provide a continuous supply of fresh, approximately half expanded, immature leaves. Weevils were transferred to new containers weekly. Dead males were replaced with a male of the same source and age. When same age males were not available, younger males of the same population were used. When a female died, data collection for the container was terminated.

Egg production patterns. The purpose of this experiment was to assess the egg production patterns of each population. Each population was placed as pairs in cages within 1 d of capture or receipt as described above. The number (n) of females monitored in each population is indicated in Table 1. Each container was provided with a wax paper oviposition strip as previously described. Egg masses were removed daily, the eggs in each mass were counted, and the eggs were discarded. Each population was monitored until the last of its females died.

Egg deposition and viability. The purpose of this experiment was to determine if a male was necessary for egg deposition, egg development, and egg hatch. For phase 1 of this experiment, virgin weevils from the laboratory population were caged to provide 10 replicates of each of the following treatments: one male and one female; one female; and two females per container. Each container was set up as previously described. Egg masses were removed daily. Eggs were counted and each mass was placed individually between heat-sealed 20 × 40 mm plastic strips separated with a 2 mm long plastic straw and provided with 20 µl of glass-distilled, deionized water. Preliminary experiments established that eggs from gravid, fertilized females held in unsealed Petri dishes (100 mm × 15 mm) either between egg laying strips or between citrus leaves had a hatch rate of 58 ± 2% at 30°C (n = 100 egg masses). Eggs from gravid, fertilized females sealed in plastic with water as described above had a hatch rate of 92 ± 7% (n = 100 egg masses). Egg masses were held at 30°C in a temperature-controlled incubator monitored daily with a mercury thermometer. Egg masses were checked for hatching daily for 14 d after deposition. After 59 d, phase 2 of this experiment was begun. Males were removed from the male-female treatment and placed with the females in the single female treatment. The females from the phase 1 female-male treatment were discarded. The new female-male pairs and the treatment with two females were monitored for egg production and egg hatch for an additional 13 d. Holding conditions and other methods were the same as phase 1.

Statistical analyses. Means in Table 1 were compared using the GLM procedure and Tukey's Studentized Range (HSD) test (SAS 1996). Relationships between female age vs egg production, egg mass production, and eggs per mass were assessed using correlation analysis and with ANOVA, LSMEANS, PROC CORR, and PROC GLM (SAS Institute, Inc. 1990).

Results and Discussion

Egg production pattern. These data are presented in Tables 1 and 2 and Figures 1-4. The laboratory groups differed statistically from one another only for mean days before an egg mass (6.5 vs 0.3 d; Table 1). That is, virgin females took longer to

Table 1. Egg production pattern. Population egg laying pattern summary*

Population	n**	Mean days lived	Mean reproductive days	Non-reproductive days before death	Mean egg masses	Mean days between egg masses
Laboratory						
Laboratory 1 (mated)	20	152 ± 65 ab	119 ± 57 ab	12.4 ± 11.3 a	101 ± 65 ab	2.2 ± 0.8 a
Laboratory 2 (virgin)	40	164 ± 67 a	137 ± 56 a	21.8 ± 35.9 a	117 ± 56 a	1.9 ± 0.5 a
Field						
Homestead	39	130 ± 83 ab	133 ± 70 a	14.2 ± 9.8 a	67 ± 46 bcd	2.2 ± 0.7 a
Lake Alfred	25	123 ± 60 ab	112 ± 57 abc	10.9 ± 9.3 a	82 ± 44 abc	2.0 ± 0.7 a
Mt. Dora	20	54 ± 53 cd	42 ± 41 de	11.6 ± 15.2 a	38 ± 35 cde	1.7 ± 0.6 a
Southport	20	82 ± 76 bc	72 ± 65 bcd	9.3 ± 19.9 a	35 ± 38 de	3.2 ± 1.4 b
Vero Beach	20	78 ± 39 bcd	63 ± 36 cde	15.4 ± 14.6 a	46 ± 28 de	2.1 ± 0.7 ab
Laboratory						
Laboratory 1 (mated)	20	0.9 ± 0.3 ab	6514 ± 182 ab	54 ± 19 abc	68 ± 13 ab	0.3 ± 0.7 a
Laboratory 2 (virgin)	40	0.9 ± 0.3 ab	9649 ± 4833 a	74 ± 27 a	79 ± 10 a	6.5 ± 2.6 d
Field						
Homestead	39	0.6 ± 0.2 bc	4306 ± 3268 bcd	36 ± 18 bcd	55 ± 31 abc	3.2 ± 2.4 b
Lake Alfred	25	0.8 ± 0.3 abc	4570 ± 3144 bc	40 ± 13 bcd	56 ± 17 abc	2.7 ± 2.6 bc
Mt. Dora	20	1.0 ± 0.3 a	1326 ± 1230 de	35 ± 9 cd	37 ± 9 c	0.3 ± 0.7 a
Southport	20	0.5 ± 0.2 c	1518 ± 1575 cde	25 ± 12 d	51 ± 20 bc	3.0 ± 2.7 b
Vero Beach	20	0.7 ± 0.3 bc	2135 ± 1401 cde	32 ± 9 d	47 ± 15 bc	1.0 ± 1.9 bcd

* Means ± standard deviation. Means followed by the same letter are not different by the GLM Procedure and Tukey's HSD test, $\alpha = 0.05$.
** n = number of females.

oviposit their first egg mass compared to mated females. The 20-d reproductive age difference between the laboratory groups was reflected in their other means (Table 1). For example, the laboratory groups differed in mean days lived by 12 d, in mean reproductive days by 18 d, and by 9 non-reproductive days before death (Table 1).

We examined age distribution by graphing survival time vs number of females for each group (Fig. 1). Laboratory 2 was known to be the youngest group and had survival times ranging from 22 to 330 d (Table 2) and mean survival of 164 ± 67 d

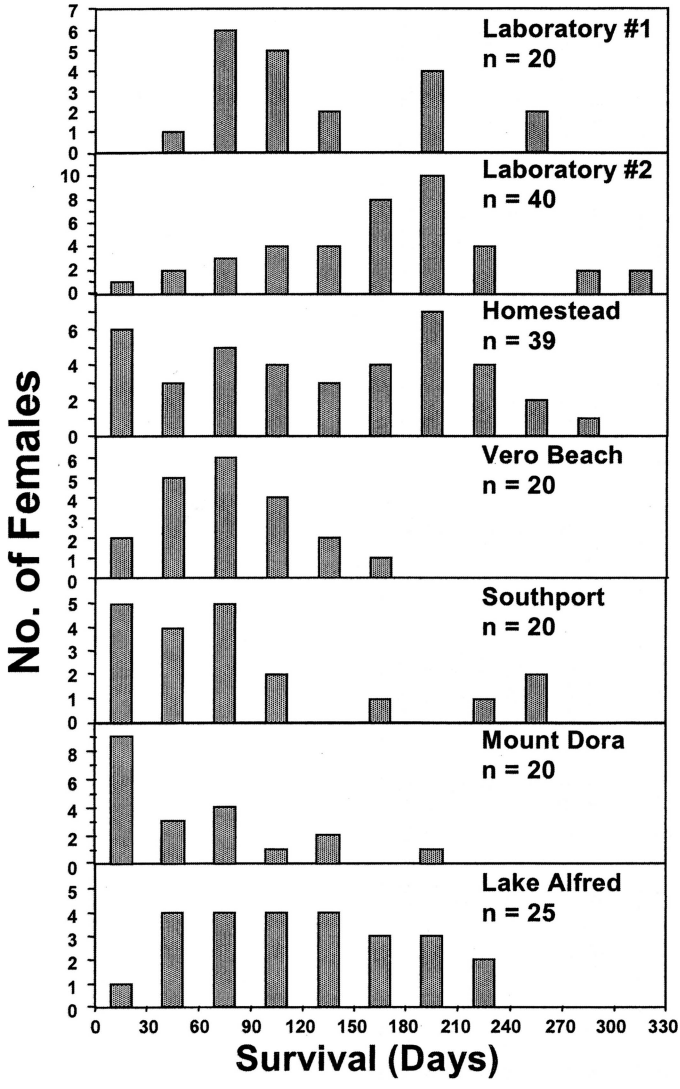

Fig. 1. Frequency distributions for the survival days of females from each population in egg production pattern experiment.

Table 2. Egg production pattern. Range of *Diaprepes abbreviatus* population oviposition patterns

Population	n	Individual			Days between egg masses	Egg masses/ reproductive days	Total eggs/ female	Eggs/ reproductive days	Eggs/ egg mass
		Days lived	Reproductive days	Egg masses					
Laboratory									
Laboratory 1 (mated)	20	41-268	32-240	28-265	1-50	0.4-1.5	1,535-19,826	34-112	52-88
Laboratory 2 (virgin)	40	22-330	19-237	15-246	1-24	0.5-1.4	1,042-20,048	29-130	35-117
Field									
Homestead	39	3-300	0-269	0-161	1-28	0.2-1.1	0-10,215	1-82	4-110
Lake Alfred	25	22-231	16-220	6-181	1-18	0.3-1.4	532-11,414	24-65	20-93
Mt. Dora	20	9-192	1-136	1-112	1-11	0.6-1.6	32-4,561	21-52	19-63
Southport	20	10-243	6-224	4-138	1-42	0.2-0.8	166-6,877	7-52	24-91
Vero Beach	20	27-159	10-136	4-110	1-15	0.3-1.2	160-5,456	13-51	30-81

(S.D.) (Table 1). For a field population, Homestead most resembled the survival distribution of laboratory 2 (Fig. 1), had a survival time range from 3 to 300 d (Table 2) with a mean survival of 130 ± 83 d (Table 1). Although not different in mean days lived from either Homestead or the laboratory groups, Lake Alfred (123 ± 60 d) (Table 1) had a somewhat different survival distribution compared to Homestead and laboratory 2 (Fig. 1). The survival distributions indicated that the Lake Alfred and Homestead field populations contained a greater proportion of younger, virgin females than the other field collections, a conclusion also supported by mean survival times that were not different than the laboratory groups (Fig. 1, Table 1). In fact, the means for the Lake Alfred and Homestead populations were not different from the laboratory group means in almost every respect (Table 1). By comparison, the Vero Beach population was short-lived and did not appear to contain young females perhaps because Vero Beach weevils were collected about 30 days past peak fall emergence (Fig. 1, Table 1). Compared to Lake Alfred, Homestead and Laboratory 1 and 2, Mt. Dora, and Southport weevils lived fewer days, had fewer reproductive days, fewer egg masses, and fewer mean total eggs (Table 1).

As discussed above, days to first egg mass effectively distinguishes young, virgin females from older mated females. Figure 2 presents the distribution of days to first egg mass for each population. Based on this distribution, Homestead, Lake Alfred, Vero Beach, and Southport field populations contained virgins; the Mt. Dora and Vero Beach field population did not (Fig. 2). An association between the number of days to the first egg mass and the number of days that a female survived in the experiment (Fig. 3; ANOVA: $F = 3.16$, df = 7,206, $P = 0.0034$) indicated that there were younger females in Homestead, Lake Alfred, Vero Beach and Southport populations. Although the mean total eggs for field populations were often similar (Table 1), the upper range of the reproductive capacity of each population in Table 2 reflects the survival age distribution in Figure 1.

The number of egg masses and the total number of eggs are important for pest management of *D. abbreviatus*. The number of egg masses could relate to the number of trees infested by one female but this would also depend on their egg mass distribution behavior, which is currently unknown. The number of egg masses and number of eggs/mass could relate to the number of larvae entering the soil beneath a tree canopy. For example, we estimated the range of larvae falling to the soil beneath a tree in a *D. abbreviatus* infested citrus grove as 955 to 7,290 over about one year (Nigg et al. 2003). A single female from any population studied here could potentially oviposit within this range (Table 1).

Egg production, eggs per egg mass, and number of egg masses declined with age for the laboratory group (Fig. 1), in agreement with similar declines in other insects (Godfray 1987, Godfray et al. 1991, Roff 1992). These data indicate that lower egg production in the field populations was probably related to the relative age distribution of the females in those populations. However, these data could have been related to diet or other environmental factors; or genetic-based population differences.

The upper ranges in Table 2 for total eggs for Homestead (10,215) and Lake Alfred (11,414) are about 50% more than Wolcott's (1936) most productive female (7,046 eggs) and about twice Beavers (1982) mean estimate of 6,517 eggs (no maximum given). Laboratory-reared weevils in the present study produced a maximum of 20,048 eggs by one female (Table 2), which was more than the maximum for any female from a field population. Laboratory weevils may have been selected for high egg production, because of the output oriented nature of laboratory colony operations

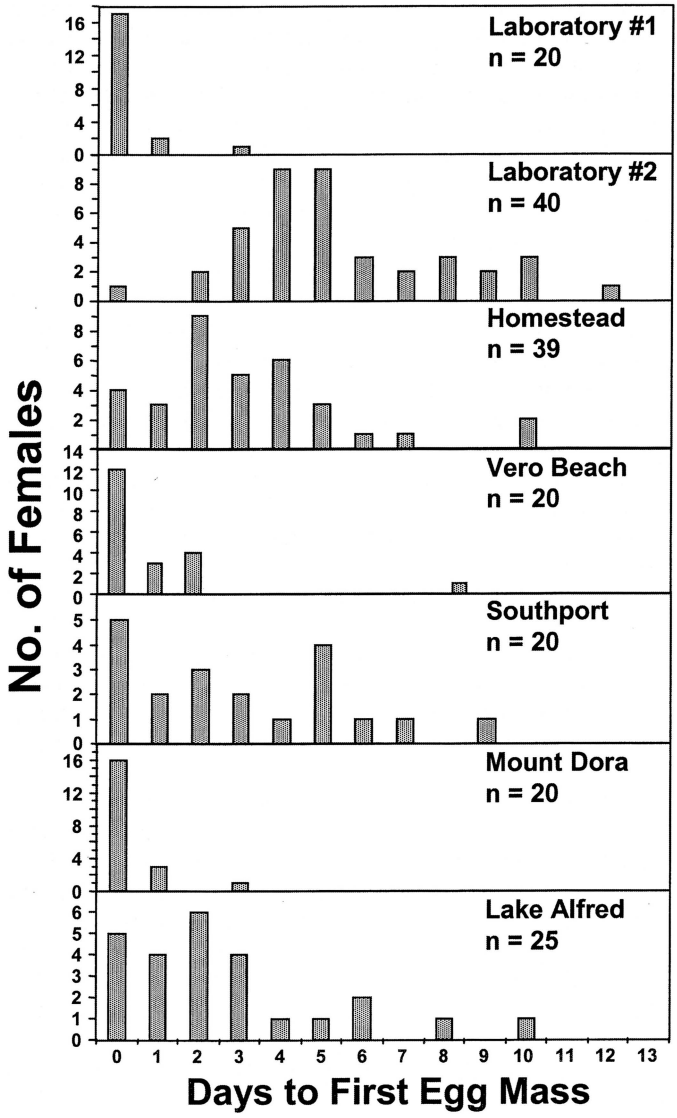

Fig. 2. Frequency distribution for the days to first egg mass deposition for each population in egg production pattern experiment.

(Lapointe and Shapiro 1999). For example, the laboratory 2 group produced a mean of 9,649 eggs, more than twice the mean egg production of Homestead and Lake Alfred, populations which resembled the laboratory population in other respects (Tables 1, 2). The originators of the laboratory colony reported the possibility of selecting eggs from *D. abbreviatus* adults that mature in the shortest possible time for

Table 3. Egg deposition. Phase 1. Orlando laboratory virgin weevil oviposition summary (Mean ± SD, n = 10)

Group	n	Egg masses	Total eggs	Mean eggs per mass	Mean % hatch	Days to 1st egg mass
Phase 1						
One virgin female per container (59 d)	10	28 ± 16	2044 ± 1318	89 ± 32	0 ± 0	4 ± 3
Two virgin females per container	10	38 ± 26	2621 ± 1733	70 ± 32	0 ± 0	5 ± 7
One virgin male/one virgin female per container	10	46 ± 21	4031 ± 1872	83 ± 42	66 ± 44	1 ± 2
Phase 2						
One male*/one female per container (13 d)	7	7 ± 4	667 ± 439	85 ± 61	53 ± 50	2 ± 1
Two virgin females per container	9	7 ± 5	643 ± 525	54 ± 54	0 ± 0	3 ± 1

* Male supplied to single virgin females after 59 d.

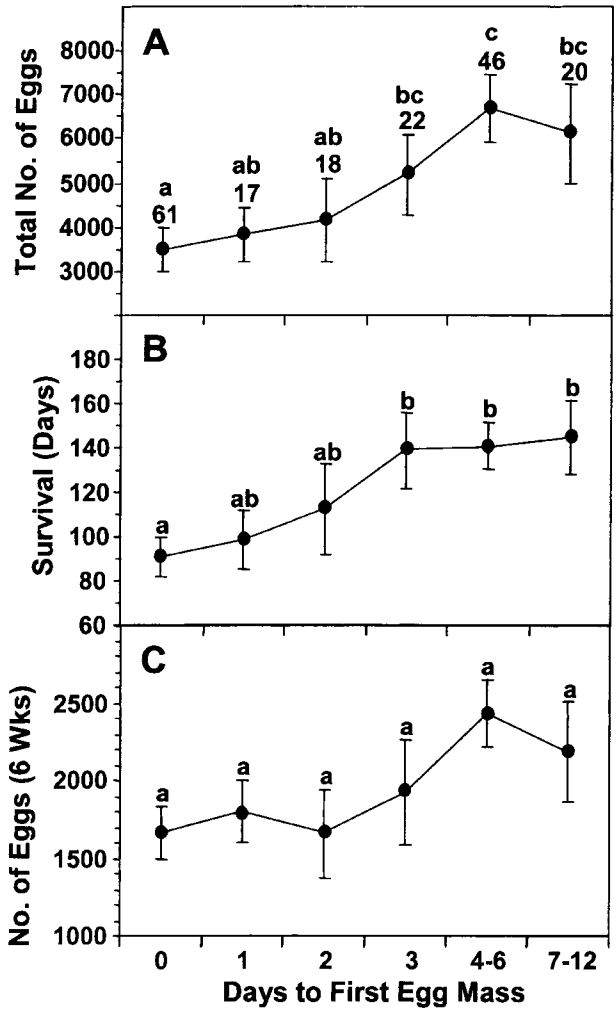

Fig. 3. Comparison of total eggs (A), survival (B) and (C) total eggs in the first 6 wk (C) for all females as a function of days to first egg mass. Means with common letters are not significantly different at the $P = 0.05$ level. The numbers associated with the means (A) are sample sizes for (A), (B) and (C).

a laboratory colony (Beavers and Selhime 1975). Laboratory adaptations of various kinds have been noted with other organisms (Styer and Greany 1983, Roush 1990a,b, Hopper et al. 1993).

Weevils captured in citrus plantings and on citrus trees most likely fed on citrus roots as larvae. However, the very wide host range of *Diaprepes* (Simpson et al. 1996) raises the possibility that larvae might have fed on roots of another species. The Homestead population undoubtedly fed as larvae on roots of species other than

citrus as almost every plant species in the ornamental plant nursery where they were collected was a life cycle host. Larval diet can be a confounding factor for the comparison of population oviposition biology. For example, adult fecundity in some insects has been shown to be influenced by larval diet (Pencoe and Martin 1982) but was not affected by larval diet in other studies (Thompson 1975, Delisle and Hardy 1997, Safonkin and Triseleva 1998, Dindo et al. 1999, Hou et al. 2000). In some cases, larvae reared on natural hosts resulted in females with greater fecundity than those from larvae reared on artificial diets (Thomas 1993). In fact, citrus may be a poor larval host as only 90 adults were recovered from 16,000 larvae seeded in 1,100 potted citrus seedlings (Beavers and Selhime 1975).

Egg deposition. Eggs neither developed nor hatched for single virgin females or paired virgin females; only for females paired with a male (Table 3). In phase 2, when single, virgin females that had laid non-viable eggs in phase 1 were paired with males, four of seven females oviposited eggs which developed into first-instar larvae (Table 4). Females paired with females continued to oviposit, but no egg developed or hatched. Two females failed to lay eggs, one paired with a male and one caged alone (Table 3), and three females paired with females failed to oviposit in phase 2 of the egg deposition experiment (Table 3). Beavers (1982) noted that 10 virgin females laid eggs which did not hatch, but did not determine if these females could lay viable eggs after mating. From our data, mated females may oviposit eggs which do not hatch or may not oviposit even with ideal conditions (Table 3). Our data confirmed that *D. abbreviatus* females require fertilization by a male for production of viable eggs.

The goal of these experiments was to determine the reproductive potential of *D. abbreviatus* field populations. There appear to be two experimental approaches for this kind of determination. One is to collect field insects, feed them natural host materials and monitor egg production. This design provided the 5,000 mean egg production estimate of Wolcott (1936) and was the approach taken in this study. A second approach is to collect field insects, allow them to lay eggs, rear the larvae on a natural or artificial diet, and determine the egg production of these adults. We avoided the artificial diet design due to possible effects of larval diet on adult biology (see above). Our data, produced with the Wolcott (1936) experimental design, but with a larger and more diverse sample of weevils, indicated that Wolcott's estimate of a mean lifetime reproductive potential of 5,000 eggs (7,046 maximum) might be relatively low, and a reproductive potential of up to 11,000 eggs for individuals in a field population might be more realistic (see Homestead and Lake Alfred, Table 2). However, the realized field potential could be lower than either 5,000 or 11,000 eggs. Two studies indicated that adult *D. abbreviatus* live only about 6 wk in the field (Beavers and Selheime 1978, Nigg et al. 2001). During the first 6 wk of our experiment, females produced an average of 1,954 eggs (SE = 102, n = 184), and there was no significant difference in egg production during this period across populations (Fig. 3C; i.e., 0, 1, 2, 3, 4-6, or 7-12 d; ANOVA, F =1.97; df = 5, 178; P = 0.0847). That is, there were no differences in mean egg production (range = 1,500 to 2,500) for any population over their initial 6 wk in the laboratory (Fig. 3C). Given a 6-wk field life expectancy, 2,000 eggs might be the best estimate of realized reproduction by individual feral *D. abbreviatus* females in field populations.

Diaprepes abbreviatus has proven difficult to control (McCoy and Simpson 1994). In Florida, adults can emerge from the soil at any time during the year but there is often a strong emergence peak associated with early spring rains, continuing high emergence through the summer, a secondary emergence peak in the fall, and low

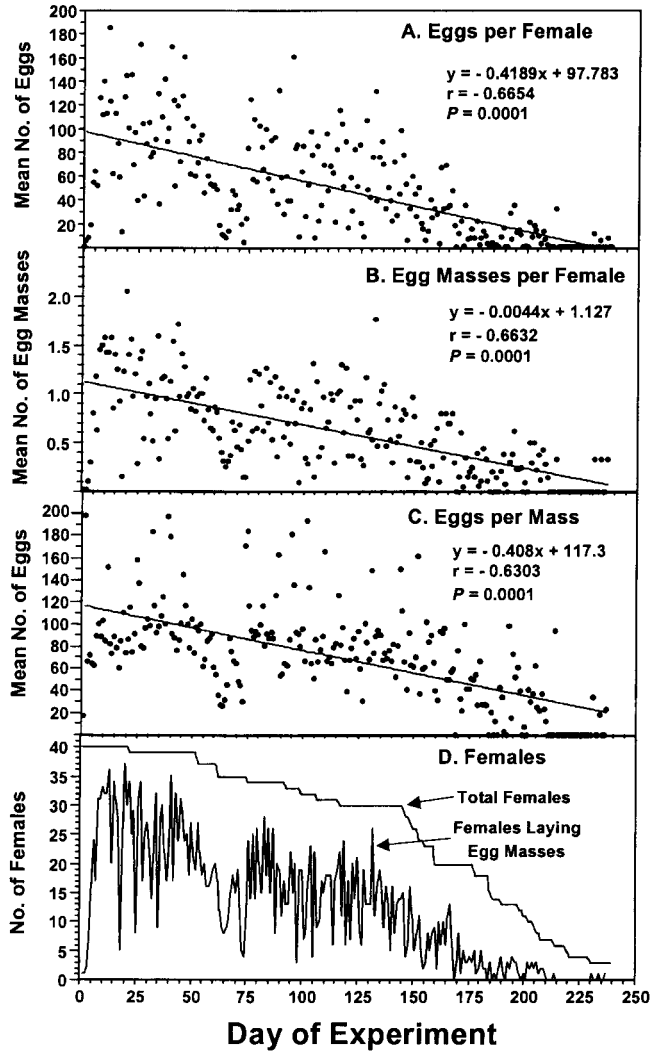

Fig. 4. Temporal relationships for egg production by females in the laboratory 2 group through to the final egg mass that was laid (Day 237) in egg production pattern experiment showing that, as females age, there was a decline in the mean number of eggs laid per female (A), the mean number of egg masses laid per female (B), and the mean number of eggs laid per egg mass (C). Means for the number of eggs laid per female per day (A) and the number of egg masses laid per female per day (B) were calculated for the total number of living females in the experiment on those days (D); whereas means for the number of eggs per egg mass per day (C) were calculated as the mean of the means for all females that laid eggs on particular days (D). Correlation coefficients (r) and *P* values indicate the results of correlation analyses using PROC CORR (SAS, 1990), and the equation for the resulting regression lines are also given.

emergence during the drier winter months (Nigg et al. 2001, 2003, Futch 2002, McCoy et al. 2003). However, the precise pattern of emergence can vary considerably and often unpredictably for different locations and years (Nigg et al. 2001, 2003, Futch 2002, McCoy et al. 2003). Females oviposit and neonate larvae hatch and enter the soil whenever adults are present, but this activity ceases with the onset of the cooler winter months when adults, egg masses, and hatching neonates are generally not detectable within groves (Nigg et al. 2003, McCoy et al. 2003). The prolonged emergence, egg-laying, and egg-hatching periods for this weevil, combined with the longevity and high fecundity of the adults as shown in the present study, contribute to control difficulties; and effective management will likely require an integrated program of persistent adult control and effective biological control for eggs in the canopy and larvae in the soil (where no registered chemical controls are currently available). Further research on adult movement, longevity, and egg distribution behavior in the field is necessary to provide a more complete picture of the population biology of this weevil and insight on when and where to apply control measures.

Acknowledgments

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