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Effect of temperature on life history of *Quadrastichus haitiensis* (Hymenoptera: Eulophidae), an endoparasitoid of *Diaprepes abbreviatus* (Coleoptera: Curculionidae)

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Abstract

The influence of temperature on life history traits of the egg parasitoid *Quadrastichus haitiensis* (Gahan) (Hymenoptera: Eulophidae) was investigated in the laboratory on eggs of the root weevil *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae). Duration of development from egg to adult decreased from 39.99 ± 0.27 days to 13.57 ± 0.07 days (mean $\pm$ SE) as temperature increased from 20 to 33 °C, respectively. No development was observed at 5–15 °C. Fecundity was highest at 25 and 30 °C (70–73 eggs per female) but was reduced at 33 °C (21.5 eggs per female). Oviposition rate was also reduced at 33 °C. *Q. haitiensis* accepted host eggs from 0 to 7 days old for oviposition but was most prolific when parasitizing 1- to 4-day-old eggs. Very few adult *Q. haitiensis* emerged from host eggs that were 5–7 days old, however, *D. abbreviatus* egg mortality was similar for eggs 0–7 days old. A brief description of the parasitoid egg, larva, prepupa, and pupa is provided.
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1. Introduction

The *Diaprepes* root weevil, *Diaprepes abbreviatus* L., is a Curculionidae endemic to the Caribbean islands that was first detected in Florida during the 1960s (McCoy and Simpson, 1994; Woodruff, 1968). This weevil is a highly polyphagous species (Grafton-Cardwell et al., 2004; Simpson et al., 1996) and currently a pest of major importance in Florida citrus and certain ornamental and root crops (Mannion et al., 2003; McCoy, 1985; McCoy and Simpson, 1994; Simpson et al., 1996). Adult weevils feed on young, tender foliage, and heavy infestations can completely defoliate young trees. Larvae feed underground, causing severe damage to root systems. Mated females lay egg masses in concealed sites, usually between two adjacent leaves that are sealed together with a gelatinous cement secreted during oviposition (Browning et al., 1995).

Considerable research in Florida has been directed toward developing management strategies for *D. abbreviatus* (McCoy, 1985; McCoy and Simpson, 1994). Efforts to establish biological control by parasitoids began during the 1970s with releases of the endoparasitoid *Quadrastichus* (*Tetrastichus*) *haitiensis* (Gahan) (Hymenoptera: Eulophidae) (Beavers et al., 1980; Sutton et al., 1972). *Q. haitiensis* failed to establish (Beavers and Selhime, 1975; Hall et al., 2001) at that time, but efforts to establish the parasitoid were reinitiated in 1997 (Peña et al., 2005). *Q. haitiensis* was originally described from specimens reared from eggs of *Exopthalmus quadrivitattus* Schauff (Coleoptera: Curculionidae) from Port-au-Prince, Haiti (Schauff, 1987). It is a primary egg parasitoid that has been reared from *D. abbreviatus* and *Pachnaeus litus* (Germar) (Coleoptera: Curculionidae)

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(Armstrong, 1987; Schauff, 1987). According to Van Whervin (1968), it is also the most common parasitoid of citrus weevil eggs in Jamaica and at times may parasitize up to 100% of the weevil egg masses in local areas. The parasitoid has also been collected from the Dominican Republic, Puerto Rico, Andros Island, and Cuba (Schauff, 1987). During 1998, the parasitoid was collected in Puerto Rico from *Diaprepes* spp. eggs (Peña et al., 2005). Subsequently, releases of *Q. haitiensis* were made beginning in 2000 into citrus and ornamental fields in Florida. The parasitoid is now established in southern Florida (Miami-Dade County) in open-field ornamental plant nurseries, but it has failed to establish elsewhere (Peña et al., 2005). Clues to determining why the parasitoid failed to establish in other geographical areas in Florida may be gained from knowledge of the biology and life cycle of the parasitoid, information that is presently lacking. The objective of the investigations reported here was to determine the effect of temperature on the life history of *Q. haitiensis* under controlled laboratory conditions, as a means of evaluating the suitability of this parasitoid as a biocontrol agent of *D. abbreviatus* in Florida.

2. Materials and methods

Stock colonies of both *D. abbreviatus* and *Q. haitiensis* were held in a room maintained at 26.5 ± 1 °C, 12:12 L:D, and approximately 78% RH. Unless otherwise stated, the same environmental conditions applied to the assays.

2.1. Rearing of Diaprepes abbreviatus

Colonies of Diaprepes root weevils were obtained from ornamental fields near Homestead, FL (80.2°W long., 25.3°N lat., 1 m alt.). Weevils were placed in $30 \times 30 \times 30$ cm Plexiglas cages with water and foliage of *Conocarpus erectus* L. (Myrtales: Combretaceae) which provided a food source and an oviposition substrate. Wax paper strips (3×10 cm) stapled together were also used as an oviposition substrate as described by Étienne et al. (1990).

2.2. Rearing of Quadrastichus haitiensis

A colony of *Q. haitiensis* was initiated in Homestead from a colony maintained at the Florida Department of Agriculture and Consumer Services, Gainesville, FL. Voucher specimens of *Q. haitiensis* were retained by the Department of Agriculture, Gainesville, FL.

2.3. Assessment of oviposition substrates

To establish the oviposition substrate for our assays, a preliminary trial was conducted to determine if there was any difference in parasitism when *Q. haitiensis* was offered 1-day-old *D. abbreviatus* egg masses either concealed between *C. erectus* leaves, concealed between wax paper strips or non-concealed in wax paper strips (one strip removed). Seventeen weevil egg masses of each treatment

were offered in a choice situation to 250 2- to 3-day-old pairs of *Q. haitiensis*. Parasitoids were introduced into a Plexiglas cage (as described above). The parasitoids were provided pure honey (streaked on paper placed on the inside wall of the cage) and water (dispensed through a saturated cotton wick in a vial placed on the bottom of the cage). Branches with leaves containing *D. abbreviatus* eggs were inserted into a 100 ml plastic container filled with water and placed in the center of the cage. The wax paper strips with eggs were randomly hung from the cage wall. Host eggs were removed from the cage 1 day later and individually dissected under a microscope to assess presence or absence of parasitoid eggs. Data were subjected to one-way analysis of variance and t test was used for mean separation at $P < 0.05$ (STSC, 1987).

2.4. Influence of host egg age on parasitism

A no choice test was conducted to investigate the influence of host egg age on parasitism. *D. abbreviatus* eggs that were 1, 2, 3, 4, 5, 6, and 7 days old were exposed to *Q. haitiensis* adults. Six *D. abbreviatus* egg masses of the same age group (non-concealed on wax paper) were offered to 30 female and 10 male *Q. haitiensis* adults (1–5 days old) for 16 h. The experiment was conducted in Bell 1-L wide mouth jars, the lids had a 7-cm-diameter opening covered with fine mesh to allow ventilation. Each jar was supplied with a moist cotton wick and a smear of honey. After 16 h all *Q. haitiensis* adults were removed and each individual egg mass was placed in a 10 ml test tube. The open end of the test tube was covered with a 2-ply Kimwipes tissue to allow ventilation. The number of host eggs per egg mass, the number and sex of the emerging parasitoids, and the number of dead *D. abbreviatus* eggs were recorded. The experiment was replicated five times for each host egg age. Data were subjected to a Kruskal–Wallis ANOVA which allowed the detection of significant differences between the means ($P < 0.05$) (Statistix 8 Analytical Software, 2003).

When pierced by the female's ovipositor a distinct visible mark can be seen on the host egg after approximately 24 h. To examine the relationship between parasitoid ovipositor insertions and oviposition on different ages of host eggs, two *D. abbreviatus* egg masses were offered to 10 female and 3 male adult *Q. haitiensis* for 16 h as above. Two days after initial exposure to *Q. haitiensis* individual *D. abbreviatus* eggs were examined for ovipositor insertion marks. The experiment was repeated three times. Results were subjected to one-way analysis of variance and t test was used for mean separation at $P < 0.05$ (STSC, 1987). Additionally, 10 marked eggs from each age of *D. abbreviatus* egg mass were dissected to determine if oviposition had taken place.

2.5. Assessment of development and biometrics

Five hundred adult parasitoids 1–7 days old, which were provided water and a dab of honey, were released into a

Plexiglas cage similar to the ones described above. One hundred and eighty egg masses (less than 24-h old) containing between 17 and 86 *Diaprepes* weevil eggs were then placed into the cage and left for 6 h. Afterward, egg masses were removed and placed in sets of six into separate 1-L Bell glass jars. These jars were transferred to an incubator set at the corresponding experimental temperature and a photoperiod of 16:8 (L:D) h. Six different temperatures were tested: 5, 15, 20, 25, 30, and 33 °C. At various time intervals, one egg mass was removed from each jar. Eggs were counted and dissected, and the size of each immature stage was measured under a microscope. Observations of parasitized eggs continued until adult emergence, and development times (y) for each stage were established. Emerging parasitoids were sexed. Results were subjected to the non-parametric Kruskal–Wallis ANOVA ($P < 0.05$) (Statistix 8 Analytical Software, 2003).

2.6. Temperature thresholds and thermal constant

Insects require a certain amount of heat to develop (Andrewartha and Birch, 1954). The amount of accumulated heat is invariable (i.e., combination of temperature between thresholds and time is always the same) and is known as the thermal constant and is often expressed in degree-days (°D). For each temperature treatment, developmental rates (y^{-1}) were calculated. These rates were plotted against temperatures and fitted with modification 2 of the Logan model for non-linear regression (Lactin et al., 1995; Logan et al., 1976): $r(T) = e^{\rho T} - e^{[\rho T_{max} - T_{max} - T/\Delta]} \pm \lambda$, where $r(T)$ is development rate at temperature T, T_{max} is the temperature of maximal development rate, and ρ, Δ, and λ are fitted parameters.

Upper temperature threshold and maximal development rate were estimated from the regression. Because the model is considered unrealistic for estimating lower temperature thresholds (Logan et al., 1976), this was estimated from a linear regression.

Based on the lower temperature threshold obtained, the thermal constant required for egg to adult development was calculated by use of the following equation (Varley et al., 1974): $K = \sum[y_i(t_i - x)]/n$, where K is the thermal constant, y_i is the development time, t_i is the temperature, x is the lower temperature threshold, and n is replicates.

Regression curves were fitted by iterative nonlinear regression (STSC, 1987).

2.7. Fecundity and longevity

To measure the potential fecundity and longevity of *Q. haitiensis* at two different temperatures (25 and 30 °C), individual pupae of *Q. haitiensis* were placed into individual gel capsules until parasitoid emergence. Adults were sexed and newly emerged females and males were placed in couples ($n = 10$ per temperature) in ventilated 50 ml plastic vials with honey diluted in water at approximately 5%. Newly

oviposited weevil egg masses were offered daily to each pair of parasitoids until the female parasitoid died. Males were replaced as needed. Host egg masses that had been exposed to the parasitoids were dissected daily and number of eggs deposited per weevil egg was recorded. Data were subjected to either one- or two-way analysis of variance and *t* tests were used for means separation at $P < 0.05$ (STSC, 1987). If necessary, data were transformed $x * \ln(x)$ before the analysis to meet the assumption of normality and homogeneity of variance.

2.8. Demographic parameters

Previously determined biological parameters were combined to calculate the intrinsic rate of increase (r_m), net reproduction (R_o), and generation time (T) at each temperature (Birch, 1948; Southwood and Henderson, 2000) using the following equation for r_m estimation: $\sum \exp^{(-r_m x)l_x m_x} = 1$, where l_x was the survivorship of the original cohort at age x and m_x was the number of female offspring produced per surviving female in each age interval. Because immature mortality could not be measured experimentally, different estimates of this parameter (1.0, 0.8, and 0.6) were used in our calculations.

3. Results

3.1. Assessment of oviposition substrates

Results showed that the ratio between the number of eggs deposited by *Q. haitiensis* and the number of *D. abbreviatus* eggs per egg mass was highest (0.77:1) when host eggs were concealed in *C. erectus* foliage (Table 1). This ratio was reduced by 41.6% if host eggs were left non-concealed in wax paper strips and further reduced by 94.8% if eggs were left concealed in wax paper (Table 1). Despite the observed reduction, wax paper strips with host eggs were separated to expose the eggs to facilitate both the rearing system and the assessment of our bioassays.

Table 1
Oviposition of *Q. haitiensis* females offered either concealed or non-concealed egg masses of *D. abbreviatus* on different substrates (means ± SE)

Substrate	Mean number of *D. abbreviatus* eggs/mass (A)	Mean number of *Q. haitiensis* eggs/weevil egg mass (B)	B/A
C. erectus leaves (concealed host eggs)	66.93 ± 6.57 a	51.57 ± 8.92 a	0.77
Wax paper with non-concealed host eggs	51.86 ± 5.35 ab	23.43 ± 4.08 b	0.45
Wax paper with concealed eggs	45.00 ± 3.84 b	1.64 ± 0.44 c	0.04

Means within each column followed by the same letter were not significantly different (LSD, $\alpha = 0.05$).

3.2. Influence of host egg age on parasitism

Quadrastichus haitiensis oviposited in *D. abbreviatus* eggs of all ages from 0 to 7 days old (Table 2). Oviposition occurred 80% of the time in 7 days old *D. abbreviatus* eggs in which the ovipositor was inserted, to a maximum of 95% in 2-day-old host eggs (Table 3). Overall *D. abbreviatus* egg mortality was highest on eggs exposed at 4 days old, all other egg ages suffered similar mortality ($F = 3.57$; $df = 6, 203$; $P = 0.002$) (Table 2). Significantly more *Q. haitiensis* completed development when oviposition occurred in host eggs 2–4 days old, fewest completed development on 7 days old host eggs ($F = 28.6$; $df = 6, 203$; $P < 0.001$). Significantly more *D. abbreviatus* eggs died without larval emergence or parasitoid emergence when exposed to *Q. haitiensis* after seven days, the fewest dead eggs were recorded on egg masses exposed when 2 and 3 days old ($F = 7.59$; $df = 6, 203$; $P < 0.001$). There was no apparent difference in the sex ratio of emerged adult *Q. haitiensis* from host eggs 0–7 days old.

3.3. Assessment of development and biometrics

Eggs of *Q. haitiensis* exposed to 5 °C did not hatch and prepupae obtained at 15 °C never reached the pupal stage (Table 4). Complete development was only observed between 20 and 33 °C. Up to 30 °C, development significantly shortened as the temperature increased (Kruskal–Wallis *T* values: 126.19, 130.50, 115.72, 600.37, and 1030.14 for egg, larval, prepupal, pupal, and total development, respectively; $P < 0.001$ in all cases). However, except for the egg stage, no significant differences were observed between 30 and 33 °C (Table 4).

The eggs of *Q. haitiensis* are translucent white, oblong, 0.28 ± 0.01 mm long ($n = 107$), typically hymenopteriform. First instar larvae are fusiform translucent white, 0.27–0.35 mm in length during the first 6.5 h. Advanced larval instars were opaque light yellowish, larval size during last instars ranged from 1.40 ($n = 24$) to 1.47 mm ($n = 12$). Newly formed prepupae were similar in shape to the larvae, but darker. Average prepupal length was 1.42 ± 0.01 mm ($n = 85$). Pupae are exarate, and yellowish translucent, with red eyes when recently formed. As they matured, the tho-rax and one-third of the lower abdomen turned dark brown-greenish.

Only one parasitoid emerged from a single host egg. The lack of multiple parasitoids maturing in single eggs suggests that gregarious parasitism is not common when host eggs are in abundance. Overall adult length for females was 1.32 ± 0.09 mm and 1.21 ± 0.07 mm for males. In both sexes, the thorax is black and the abdomen is yellowish anteriorly becoming darker to the posterior end which is gradually pointed. The adult was described in detail by Schauff, 1987. The sex ratio (female:male) during the first three days of emergence was male biased 0.12–0.40, compared to the sex ratio during the last three days of emergence: 0.60–0.63.

3.4. Temperature thresholds and thermal constant

Development rates were fit with a nonlinear regression (Lactin et al., 1995; Logan et al., 1976) (Fig. 1) $[r(T) = e^{\rho T} - e^{[\rho T_{max} - T/\Delta]} - \lambda;$ $\rho = 0.0050 \pm 0.0001;$ $\Delta = 0.4581 \pm 1.2985;$ $\lambda = 1.0820 \pm 0.0034$, estimate $\pm$ asymptotic standard error]. The upper development threshold estimated from this equation was 33.8 °C, and the maximal development rate occurred at 32.0 °C. Because the model is

Table 3
Relationship between *Q. haitiensis* ovipositor insertions and oviposition on eggs of *D. abbreviatus* 1–7 days old (means $\pm$ SE)

Host egg age (days)	Ovipositor marked eggs	
	(#)	% oviposition
0–1	5.0 ± 1.6 bc	93
1–2	19.0 ± 4.3 ab	95
2–3	16.9 ± 5.1 abc	90
3–4	20.9 ± 1.4 a	83
4–5	2.9 ± 1.4 bc	—
5–6	2.4 ± 0.9 c	90
6–7	6.0 ± 2.3 abc	80

Two *D. abbreviatus* not-concealed egg masses of the same age group (on wax paper) were offered to 10 female and 3 male *Q. haitiensis* adults for 16 h. Ten ovipositor-marked eggs were dissected from each age group.
Numbers within a column with followed by the same letter were not statistically significant ($P < 0.05$).
The number of five-day-old host eggs was inadequate to dissect marked eggs.

Table 2
Host age preference of *Q. haitiensis* females offered *D. abbreviatus* (Da) egg masses 1–7 days old (means $\pm$ SE)

Host egg age (days)	Da egg mass size (#)	Dead Da eggs (#)	Total Da mortality (#)	# *Q. haitiensis* adults emerged		
				Total	Males	Females
0–1	45.5 ± 2.7 a	4.0 ± 0.5 bc	10.5 ± 2.0 ab	6.4 ± 1.6 bc	2.6 ± 0.7 ab	3.8 ± 0.9 ab
1–2	33.7 ± 2.3 a	2.6 ± 0.4 c	14.8 ± 1.8 ab	12.2 ± 1.5 ab	5.3 ± 1.0 a	6.9 ± 1.0 a
2-3	42.4 ± 2.7 a	2.6 ± 0.5 c	14.0 ± 2.4 ab	11.4 ± 2.1 ab	4.2 ± 0.9 a	7.2 ± 1.5 a
3–4	43.9 ± 3.3 a	4.9 ± 0.9 ab	18.1 ± 2.6 a	13.3 ± 2.3 ab	4.1 ± 1.0 a	9.2 ± 1.4 a
4-5	37.9 ± 2.5 a	6.2 ± 0.8 ab	7.7 ± 1.1 b	1.6 ± 0.7 cd	0.7 ± 0.3 bc	0.9 ± 0.4 bc
5–6	43.7 ± 3.7 a	6.9 ± 1.1 ab	7.4 ± 1.2 b	0.5 ± 0.3 cd	0.1 ± 0.1c	0.4 ± 0.2 bc
6–7	43.6 ± 3.0 a	11.8 ± 1.8 a	11.9 ± 1.8 ab	0.03 ± 0.03 d	0.03 ± 0.03 c	0.0 ± 0.0 d

Numbers within a column followed by the same letter were not statistically significant ($P < 0.05$).

Table 4
Mean development time (days ± SE) of *Q. haitiensis* at different temperatures when reared on *D. abbreviatus* egg masses on wax paper strips

Stage	5 °C	15 °C	20 °C	25 °C	30 °C	33 °C
Egg	—	14.13 ± 4.09 a	3.52 ± 0.10 b	1.38 ± 0.06 c	1.32 ± 0.08 c	0.83 ± 0.00 d
Larva	—	43.69 ± 10.85 a	6.54 ± 0.09 b	4.07 ± 0.05 c	2.30 ± 0.08 d	3.08 ± 0.74 d
Prepupae	—	—	18.76 ± 0.38 a	11.01 ± 0.33 b	4.62 ± 0.26 c	5.70 ± 0.11 c
Pupa	—	—	21.23 ± 0.27 a	10.06 ± 0.14 b	8.08 ± 0.07 c	7.87 ± 0.07 c
Total	—	—	39.99 ± 0.27 a	21.07 ± 0.14 b	12.70 ± 0.07 c	13.57 ± 0.07 c
Sex ratio	—	—	0.52	0.56	0.57	0.44
No. of egg masses	28	30	30	30	30	30
No. of eggs	1558	1146	1238	1504	1657	1078

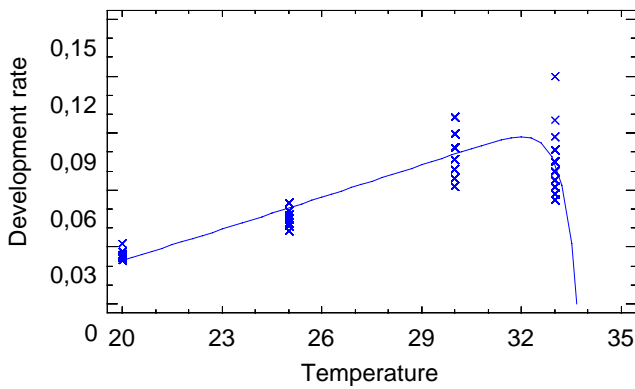Numbers within a row followed by the same letter were not statistically significant ($P < 0.05$).

Fig. 1. Development rate (days^{-1}) of *Q. haitiensis* reared on *D. abbreviatus* egg masses on wax paper strips plotted against temperature (°C). Fitted curve: Logan model and modification 2 (Lactin et al., 1995; Logan et al., 1976).

considered unrealistic for estimating lower temperature thresholds (Logan et al., 1976), development rates observed between 15 and 30 °C were further fit with a linear regression ($y = 0.0056x - 0.0904$; $R^2 = 89.0\%$; $F = 7,319.66$; $df = 1, 904$; $P < 0.00001$). The lower development threshold estimated from this equation was 16.0 °C. Using this estimate of the lower development threshold, a thermal constant for development from egg to adult of 200.5 ± 0.90 °D ($n = 1575$) was calculated.

3.5. Fecundity and longevity

Neither fecundity nor mean oviposition rate of *Q. haitiensis* females differed significantly between 25 and 30 °C (Table 5; $F = 1.52$; $df = 1, 18$; $P = 0.2235$ and $F = 0.01$; $df = 1, 18$; $P = 0.9214$, respectively). Furthermore, no differences between these temperatures were observed in the duration of pre-oviposition, oviposition, and post-oviposition periods (Table 6; $F = 0.00$; $df = 1, 18$; $P = 1$, $F = 0.81$; $df = 1, 18$; $P = 0.3801$, and $F = 1.36$; $df = 1, 18$; $P = 0.2593$, respectively). Mean longevity of adults generally decreased as temperature increased from 25 to 30 °C, this decrease was significant for males ($F = 36.20$; $df = 1, 18$; $P = 0.0001$) but not for females ($F = 3.77$; $df = 1, 18$; $P = 0.0679$) (Table 6).

Table 5
Life history parameters of *Q. haitiensis* at two different temperatures, when reared on *D. abbreviatus* egg masses on wax paper strips

	25 °C	30 °C
Fecundity (eggs)	77.60 ± 4.82	69.00 ± 5.04
Oviposition rate (eggs/day)	5.81 ± 0.73	5.73 ± 0.37

Initial number was 10 couples per temperature. No statistically significant differences were observed between temperatures.

Table 6
Mean pre-, post-, and oviposition periods and longevity (days ± SE) of *Q. haitiensis* at three different temperatures

	25 °C	30 °C
Female		
Longevity	14.50 ± 1.11	12.10 ± 0.55
Pre-oviposition	0.30 ± 0.21	0.30 ± 0.15
Oviposition	9.90 ± 0.59	8.80 ± 1.07
Post-oviposition	4.30 ± 0.68	3.00 ± 0.68
Male		
Longevity	28.40 ± 0.43 a	21.1 ± 1.47 b

Initial number was 10 couples per temperature. No statistically significant differences were observed between temperatures for females, but there were between males.

3.6. Demographic parameters

Using the results obtained at 25 and 30 °C, net reproduction (R_o), mean development time (T), and the intrinsic rate of increase (r_m) were estimated (Table 7).

Table 7
Demographic parameters at three different rates of immature survival (IS), net fecundity (R_o, females per female), generation time (T, days), and intrinsic rate of increase (r_m, day^{-1}) of *Q. haitiensis* at two different temperatures

	Temperature °C	IS = 1.0	IS = 0.8	IS = 0.6
r_m	25	0.142	0.133	0.120
	30	0.214	0.199	0.181
T	25	24.90	24.96	25.21
	30	15.86	15.91	15.92
R_o	25	34.14	27.32	20.49
	30	29.67	23.74	17.80

4. Discussion

Our results indicate that *Q. haitiensis* could successfully develop between 16.0 and 33.8 °C (lower and upper developmental thresholds, LDT and UDT, respectively). However, because the highest temperature examined was 33 °C, the estimated UDT deserves further investigation. In south and central Florida where *D. abbreviatus* is distributed, summer and winter temperatures in some areas could negatively affect parasitoid development and survival. Ambient temperatures fluctuate around 30 °C during the summer in both southern and central areas of Florida (Anonymous, 2004a). Depending on how long temperatures stay above estimated UDT, these could negatively affect this tropical parasitoid. However, it is likely that winter temperatures may be more detrimental to the parasitoid than summer temperatures. Minimum ambient temperatures during January through March in southern Florida fluctuate between 15 and 17 °C with mean temperatures

of 19–20 °C. In central Florida, minimum temperatures fluctuate between 10 and 13 °C with a mean temperature of 15 °C (Anonymous, 2004a), clearly under LDT. Given that *Q. haitiensis* has been established in southern Florida since 2001 but has failed to establish further north (Peña et al., 2005), winter temperatures are likely an important factor in the parasitoid's inability to establish in central Florida and other areas of the state. In the area of Puerto Rico where *Q. haitiensis* was collected the average temperature is 22 °C, with minimum of 19 °C (Anonymous, 2004b, 1977). However, in the mountains of Puerto Rico, minimum temperatures range from 2.8 to 5.6 °C (Anonymous, 1977). Therefore, it may be valuable to search these previously unsurveyed cool hilly areas for parasitoid biotypes which are adapted to lower temperatures.

According to Lapointe (2001), 5.5 ± 0.69 mean days are needed for *D. abbreviatus* eggs to hatch at 30 °C, and this is within the developmental range for *Q. haitiensis* eggs and larvae to develop (1.32 ± 0.08 days and 2.30 ± 0.08 days,
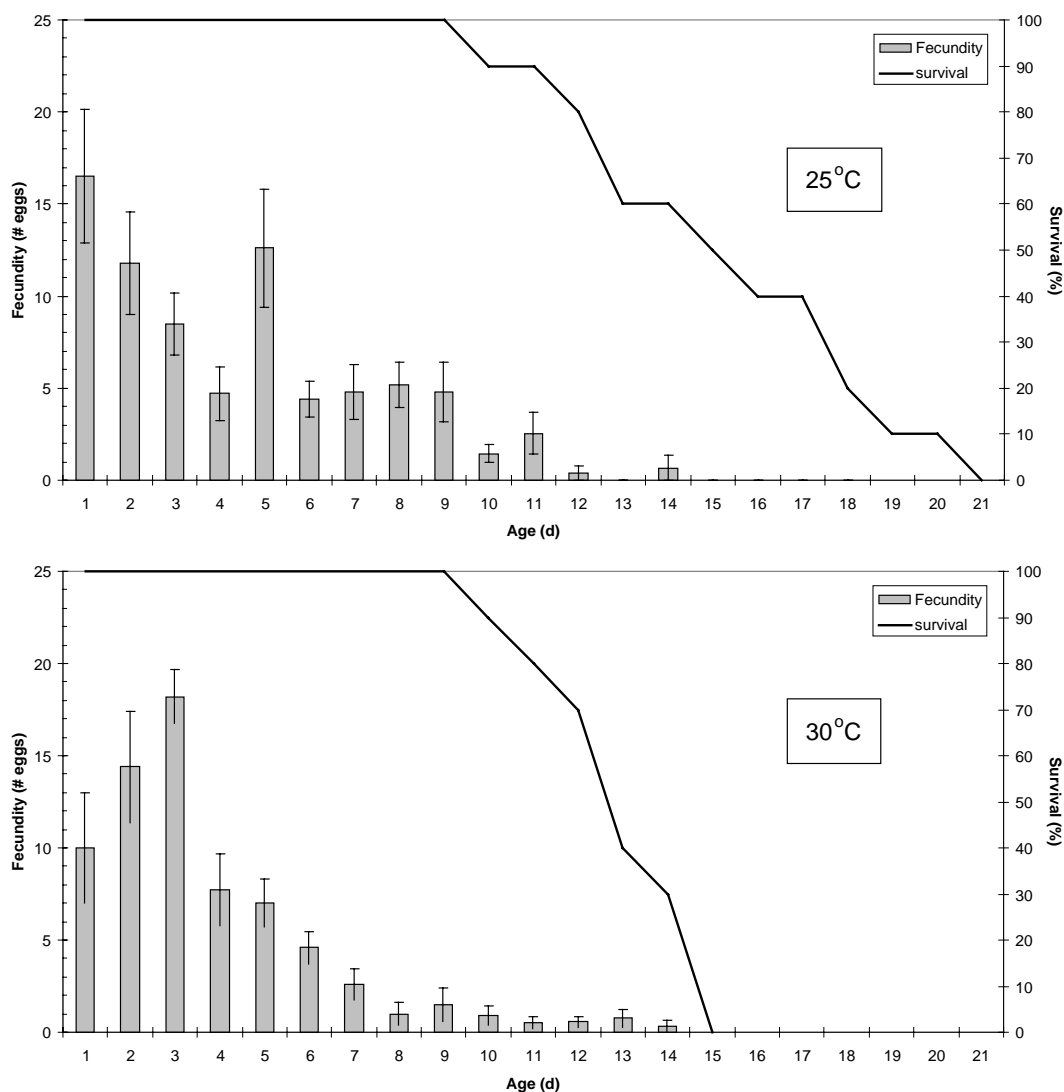

Fig. 2. Daily oviposition (# eggs per female) and survival of adult *Q. haitiensis* at 25 and 30 °C.

respectively) at 30 °C. A similar trend is observed at 20 °C, when the total time for parasitoid eggs and larvae to develop (3.52 ± 0.10 days and 6.54 ± 0.99 days, respectively) falls within the number of days required for eggs of *D. abbreviatus* to develop (Lapointe, 2001). This suggests that the parasitoid is capable of completing its development from egg to adult in synchrony with the physiology of *D. abbreviatus* eggs at temperatures fluctuating between 20 and 30 °C. Survival of *D. abbreviatus* eggs is reduced at 15 °C (Lapointe, 2001), as is the development of *Q. haitiensis* at the same temperature based on our study. Therefore, development of host egg and parasitoid could be drastically reduced in those areas where winter temperatures are closer to the lower temperature threshold for host and parasitoid species.

An additional limitation for the success of *Q. haitiensis* in Florida could be related to the window for parasitism offered by its host. Successful oviposition by *Aprostocetus vaquitarum* (Wolcott) (Hymenoptera: Eulophidae), another parasitoid of *D. abbreviatus* successfully established in southern Florida, is limited to host eggs less than 6 days old and successful development rapidly declines for hosts more than 4 days old (Jacas et al., 2005). *Q. haitiensis* is almost as exigent as *A. vaquitarum*. Although it oviposits in host eggs from 0 to 7 days old, successful development to the adult stage drops significantly when host eggs reach an age of 4 to 5 days old. Females in a no-choice situation did not differentiate between young host eggs, ideal for egg and larval development, and older host eggs which are far less suitable; oviposition occurred 80–90% of the time the ovipositor was inserted into a host egg that was 6 or 7 days old, respectively. Host eggs of all ages which were pierced by the ovipositor rarely survived. Development of *D. abbreviatus* appears to cease when parasitoid oviposition occurs but it is not clear if the host is killed by the ovipositing female or the developing parasitoid. In the present study, an abundance of host eggs of all ages was offered to *Q. haitiensis*. Successful parasitism (adults emerged) was highest on 3- to 4-day-old host eggs, which experienced 30% parasitoid emergence, but dropped to almost zero on host eggs older than five days. Though parasitoid development is generally not successful on host eggs which are more than 4 days old, the host egg is killed resulting in substantial *D. abbreviatus* mortality among all ages of host eggs exposed to this parasitoid. The few eggs where oviposition marks but no oviposition was observed may be used by *Q. haitiensis* females for feeding, as it has commonly been observed in other Eulophidae (Urbaneja et al., 2001). This is assumed to provide female wasps with resources that can be used during host searching or for egg maturation (Godfray, 1994; Jervis and Kidd, 1986).

Oviposition rate of *Q. haitiensis* females at 25 °C declined from 16.50 eggs per day for youngest females to 0.66 eggs per day for 14-day-old females. The daily reproduction of *Q. haitiensis* is shown in Fig. 2. At both 25 and 30 °C, more than 70% females began to oviposit at day 0. Similarly, more than 70% of parasitoid eggs were laid during the first five days of a female's adult life at both 25 and 30 °C. At 25 °C with an excess of host eggs available (57.52 ± 24.24), 35.2 ± 24.8% of weevil eggs were parasitized. The lack of multiple parasitoids maturing in single eggs suggested that gregarious parasitism is not common when host eggs are in abundance.

The intrinsic rate of natural increase (r_m) is a good indicator of the temperature at which the growth of a population is most favorable, because it reflects the overall effects of temperature on development and reproduction and survival characteristics of a population. For the hypothetical immature survival rates studied, the population reared at 30 °C showed the maximal values of r_m (0.181–0.214 day−1), minimal generation times (15.86–15.92 days), and maximal net fecundity (17.80–29.67 females per female) (Table 7). These r_m values are slightly lower than those obtained for *A. vaquitarum* under similar conditions (Jacas et al., 2005) but such values should not hamper the biological control of *D. abbreviatus* by *Q. haitiensis*. However, winter temperatures below 15 °C could seriously impair parasitism and development by *Q. haitiensis*, a factor which may explain the failure of *Q. haitiensis* to establish areas of Florida north of Miami-Dade County.

Acknowledgments

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