

Thermal requirements of *Fidiobia dominica* (Hymenoptera: Platygasteridae) and *Haeckeliana sperata* (Hymenoptera: Trichogrammatidae), two exotic egg parasitoids of *Diaprepes abbreviatus* (Coleoptera: Curculionidae)

Josep A. Jacas · Jorge E. Peña · Rita E. Duncan · Bryan J. Ulmer

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Abstract *Diaprepes abbreviatus* is an exotic root weevil occurring in southern US. It is a highly polyphagous species which can complete its entire life cycle on citrus and several woody ornamental plants. The lack of native egg parasitoids for this weevil in citrus orchards has triggered efforts to evaluate candidate egg parasitoids from the Caribbean Region into Florida. The egg parasitoids *Fidiobia dominica* and *Haeckeliana sperata* are two exotic natural enemies of *D. abbreviatus* recently introduced in the US in a classical biological control program. The thermal requirements of both parasitoids were studied in the laboratory. The upper development threshold (UDT) of *F. dominica* was 30.0°C, its maximal development rate (MDR) occurred at 27.6°C, its lower development threshold (LDT) was 9.6°C and its thermal constant (K) for development from egg to adult was 293.1 DD. For *H. sperata*, UDT was 35.0°C, MDR occurred at 31.0°C, LDT was around 15°C and K was 188.1 DD. Based on these results, both species would be able to complete 17 to 18 generations annually in southern Florida. However, host availability during critical periods could severely impair the ability of these egg parasitoids to establish and successfully control *D. abbreviatus* in areas where winter temperatures fluctuate around 12°C, the LDT for this pest.

Keywords Biological control · Citrus IPM · Development · Thermal constant · Temperature thresholds

J. A. Jacas (✉)

Departament de Ciències Agràries i del Medi Natural, Universitat Jaume I, Campus del Riu Sec, 12071
Castello de la Plana, Spain
e-mail: jacas@camn.uji.es

J. E. Peña · R. E. Duncan · B. J. Ulmer

Department of Entomology and Nematology, Tropical Research and Education Center, University of
Florida, 18905 SW 280th Street, Homestead, FL 33031, USA

Introduction

Diaprepes abbreviatus (L.) (Coleoptera: Curculionidae) is a root weevil indigenous to the Lesser Antilles of the Caribbean Region (Woodruff 1985) that was introduced into Florida in 1964, presumably from Puerto Rico with imported ornamental plants (Woodruff 1964). This weevil is a highly polyphagous species (Simpson et al. 1996) which can complete its entire life cycle on citrus and several woody ornamental plants (Schroeder et al. 1979). Adult *D. abbreviatus* feed along the edges of leaves, leaving characteristic semi-circular notches. Eggs are laid in the canopy, glued between two leaves. Upon hatching, larvae fall to the ground to enter the soil where they feed on the roots of host plants. Damage from root feeding can be significant, leading to reduced productivity and often to death of the host plant. Root feeding may also leave citrus plants more susceptible to root rot organisms such as *Phytophthora* spp. (Timmer et al. 2005).

Diaprepes abbreviatus has become an important pest of citrus, ornamentals and various other crops throughout much of central and southern Florida, where it is estimated to cause losses of several million dollars annually (Stanley 1996). *Diaprepes abbreviatus* has recently colonized the citrus-growing regions of Texas (Skaria and French 2001) and California (Grafton-Cardwell et al. 2004) where it is a threat to several crops.

The lack of native egg parasitoids for this weevil in citrus orchards in Florida (Hall et al. 2001), and past failures of classical biological control (Beavers et al. 1980), have triggered renewed efforts to introduce, release, and evaluate candidate egg parasitoids from the Caribbean Region into Florida (Peña et al. 1998; Peña and Amalin 2000; Hall et al. 2002; Jacas et al. 2005; Castillo et al. 2006; Ulmer et al. 2006). The egg parasitoids *Fidiobia dominica* Evans & Peña (Hymenoptera: Platygasteridae) and *Haeckeliania sperata* Pinto (Hymenoptera: Trichogrammatidae) were collected during two exploratory trips to the island of Dominica between April and June, 2003. Parasitoids were collected ex. *D. abbreviatus* and *D. doublieri* Guérin (Coleoptera: Curculionidae) eggs at an altitude of 135–360 m in Dominica, in areas where average temperature ranges from 22–26°C with night temperatures of 18–20°C. Collected specimens were introduced into the University of Florida's Tropical Research and Education Center quarantine where they have been reared for several generations on *D. abbreviatus* eggs. *Fidiobia dominica* is a solitary egg endoparasitoid (Evans and Peña 2005; Jacas et al. 2007), whereas *H. sperata* is a gregarious endoparasitoid. Releases of both parasitoids were approved by APHIS PPQ in June 2006 and releases are under way at various sites in Florida as part of the classical biological control program against *D. abbreviatus*.

The aim of this study was to evaluate the impact of a range of temperatures on *F. dominica* and *H. sperata* development as a means to predict their potential establishment and geographical range in Florida.

Materials and methods

Stock colonies

Adult *D. abbreviatus* root weevils were obtained from ornamental plant fields at Homestead, FL (80°22' W long., 25°3' N lat., 1 m alt.). Weevils were placed in plexiglass cages (30 × 30 × 30 cm) with water and foliage of the host plant *Conocarpus erectus* L. (Myrtales: Combretaceae) in a room held at 25.6 ± 1°C, 12:12 L:D, and approximately 65 ± 5% RH. The foliage was in the form of bouquets containing 20–25 terminal branches

(each 15–20 cm long and with approximately 10 leaves) placed in a 500-ml plastic container full of water. Wax paper strips (3 × 10 cm) stapled together were also used as an oviposition substrate (Castillo et al. 2006). Both foliage and paper strips were renewed every 2–3 d. Bouquets were further used for the rearing of *H. sperata*, whereas paper strips were used for *F. dominica*.

Either leaves (for *H. sperata*) or wax paper strips (for *F. dominica*) containing *D. abbreviatus* eggs were placed inside similar cages in a room held at the same environmental conditions as the host. Adults of the corresponding parasitoid were introduced into the cage and provided honey and water. Parasitized eggs were removed from the cage 2–4 d later and placed in plexiglass emergence cages (same dimensions as above) supplied with water and a honey food source until adult emergence (approximately 2 and 3 weeks for *F. dominica* and *H. sperata*, respectively).

Voucher specimens of both *F. dominica* and *H. sperata* were retained in the Florida Collection of Arthropods, Gainesville, Florida, in the US National Museum of Natural History (USNM) and in the Canadian National Collection, Ottawa, Canada.

Development

Fidiobia dominica

Half square centimeter wax paper strips containing one 20–24-h-old *D. abbreviatus* egg clutch were individually introduced into a 10 ml glass vial with three 20–24-h-old naive *F. dominica* adults. Vials were kept in an illuminated room held at $25.6 \pm 1^\circ\text{C}$. Adult wasps were removed from the vials 6 h later and the vials were kept in a climatic chamber at a 12:12 L:D photoperiod and the corresponding temperature treatment. Six different temperatures were considered: 9, 15, 20, 26, 30, and 36°C , and 30 replicates (=vials) were used for each temperature. Parasitized eggs were periodically dissected and checked under a stereomicroscope (Leica MZ6) with a cold light source (Leica CLS100). Based on these observations, the development time (y) for each stage and temperature were established.

Haeckeliania sperata

10-cm green buttonwood shoot tips with less than 1-d-old *D. abbreviatus* eggs were grouped in bouquets and placed in a 500-ml plastic container with water and exposed in plexiglass cages (same dimensions as above) to about 750 adults of *H. sperata* for 6 hours in an illuminated room held at $25.6 \pm 1^\circ\text{C}$. Shoot tips were subsequently removed, washed with water and further checked under the microscope to remove all adults. Immediately afterwards, 25 egg masses (one single shoot tip could hold from 1 to 5 egg masses) were combined in a bouquet. Six bouquets, one for each experimental temperature (10, 15, 20, 25, 30 and 35°C) were assembled. These bouquets were lodged in a moist piece of florists' sponge and placed in an 800 ml wide mouth Ball® glass jar (8.5 cm diam × 16.5 cm high) with 5 mm of water in the bottom and sealed with a fine mesh lid. Each jar was transferred to the corresponding temperature under a photoperiod of 12:12 L:D photoperiod. Parasitized egg masses were periodically checked under a stereomicroscope (Leica MZ6) with a cold light source (Leica CLS100) until adult emergence. Based of these observations, total development time (y) from egg to adult was established for each temperature.

Temperature thresholds and thermal constant

Once development times (y) were established for each temperature treatment, developmental rates ($r(T) = y^{-1}$) 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): $r(T) = e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\Delta]} - \lambda$, where: $r(T)$, development rate at temperature T , T_{max} , temperature of maximal development rate, and ρ , Δ , and λ fitted parameters. The regression curve was fitted by iterative nonlinear regression (STSC 1987). Both upper and lower temperature thresholds (UTT and LTT, respectively) were estimated from this regression. Because the model is considered unrealistic for estimating LTT (Logan et al. 1976), this parameter was also estimated from a linear regression.

Based on the LTT 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 , thermal constant, y_i , development time, t_i , temperature, x , lower temperature threshold and n , replicates.

Temperature

Mean minimum and mean maximum monthly temperatures from Miami and Lake Alfred areas were studied as representative of the central and southeast regions of Florida where releases of both *F. dominica* and *H. sperata* are taking place (Miami-Dade and Polk counties). Values were obtained from the Southeast Regional Climate Center for Miami WSCMO airport (#085663—from 1948 to 2004) and from the Citrus Research and Education Center, Lake Alfred (#084707—from 1924 to 2000). Individual months missing more than five days of temperature data were not included in the means. Mean monthly temperatures were virtually mid-way between the mean minimum and mean maximum temperatures and were not included in the figure to ease interpretation.

Results

Development

Fidiobia dominica

Eggs exposed either to 9 or 36°C did not hatch, and just 5% of prepupae obtained at 30°C reached the pupal stage (Table 1). However, these pupae did not produce any adults. Therefore, complete development was only observed between 15 and 26°C. Within this range, development shortened as the temperature increased, percent pupation did not significantly change ($F = 20.86$; $df = 3, 19$; $P < 0.0001$; mean: $87.2 \pm 4.5\%$), and both survival ($F = 41.22$; $df = 2, 27$; $P < 0.0001$) and sex ratio (female:total; $F = 9.18$; $df = 2, 22$; $P < 0.0013$) were significantly lower at 15°C than at 20 and 26°C (Table 1). Hence, adequate development was only obtained at 20 and 26°C.

Haeckeliana sperata

Eggs of *H. sperata* exposed to 10, 15 and 35°C did not hatch. Complete development was only possible between 20 and 30°C (Table 2). Within this range, development shortened as

Table 1 Mean stage-specific developmental time, days (\pm SE, n = number of individuals inspected), percentage pupation, survival and sex ratio (female:total) of *F. dominica* at different temperatures when reared on *D. abbreviatus* egg masses

Stage	9°C	15°C	20°C	26°C	30°C	36°C
Egg	–	2.6 \pm 0.1 (n = 11)	1.6 \pm 0.1 (n = 10)	0.9 \pm 0.1 (n = 17)	0.94 \pm 0.1 (n = 17)	–
Larva	–	9.3 \pm 0.3 (n = 30)	2.9 \pm 0.1 (n = 11)	2.3 \pm 0.1 (n = 19)	1.6 \pm 0.1 (n = 17)	–
Prepupa	–	12.3 \pm 0.3 (n = 50)	6.0 \pm 0.2 (n = 30)	3.2 \pm 0.1 (n = 102)	4.1 \pm 0.1 (n = 19)	–
Pupa	–	40.2 \pm 0.4 (n = 39)	17.6 \pm 0.1 (n = 333)	11.5 \pm 0.1 (n = 113)	–	–
Total	–	65.6 \pm 0.5 (n = 39)	28.3 \pm 0.1 (n = 333)	18.6 \pm 0.1 (n = 113)	–	–
Pupation*	0.0	87.0 \pm 8.7a	91.2 \pm 3.6a	84.6 \pm 6.7a	5.1 \pm 2.6b	0.0
Survival*	0.0	15.7 \pm 3.8b	82.1 \pm 6.2a	85.0 \pm 6.9a	0.0	0.0
Sex ratio	–	0.338 \pm 0.114b	0.683 \pm 0.053a	0.871 \pm 0.038a	–	–

Percentage pupation and survival and sex ratio are based on 10 egg masses per temperature

Means in each row followed by the same letter are not significantly different ($P < 0.05$)

*Data were arcsin-transformed before ANOVA

Table 2 Mean developmental time, days (\pm SE, n = number of individuals) and sex ratio (female:total) for *H. sperata* at different temperatures when reared on *D. abbreviatus* egg masses

	10°C	15°C	20°C	26°C	30°C	35°C
Mean development time	no		survival	no survival	31.2 \pm 0.1 (n = 486)	
18.8 \pm 0.1 (n = 460)			15.1 \pm 0.1 (n = 72)	no survival		
Sex ratio	no		survival	no survival	0.708 \pm 0.077a	
0.808 \pm 0.058a			0.877 \pm 0.040a	no survival		

Sex ratio values are based on 10 egg masses per temperature

Means in each row followed by the same letter are not significantly different ($P < 0.05$)

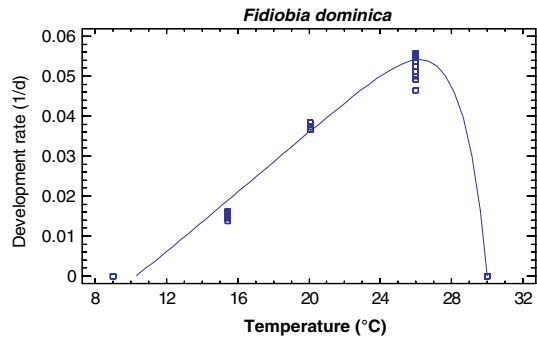
temperature increased, and sex ratio was female-biased and did not significantly change ($F = 1.53$; $df = 2, 21$; $P < 0.2404$; mean: 0.799 ± 0.038).

Temperature thresholds and thermal constant

Fidiobia dominica

Development rates were fit with a nonlinear regression (Lactin et al. 1995; Logan et al. 1976) (Fig. 1) [$r(T) = e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\Delta]} - \lambda$; $\rho = 0.0035 \pm 0.0001$; $\Delta = 0.4743 \pm 0.0540$; $\lambda = 1.0371 \pm 0.0010$, estimate \pm asymptotic standard error]. The upper development threshold (UDT) estimated from this equation was 30.0°C, and the maximal development rate (MDR) occurred at 27.6°C. Development rates observed between 9 and 26°C were fit with a linear regression ($r(T) = 0.0033 T - 0.0323$; $R^2 = 97.18\%$; $F = 9062.39$; $df = 1, 263$; $P < 0.0001$). The lower development threshold (LDT) estimated

Fig. 1 Development rate (d^{-1}) of *F. dominica* when reared on *D. abbreviatus* plotted against temperature ($^{\circ}C$). Fitted curve: Logan model and modification 2



from this equation was $9.6^{\circ}C$. Using this estimate of the lower development threshold, a thermal constant for development from egg to adult of 293.11 ± 1.73 DD ($n = 252$) was calculated.

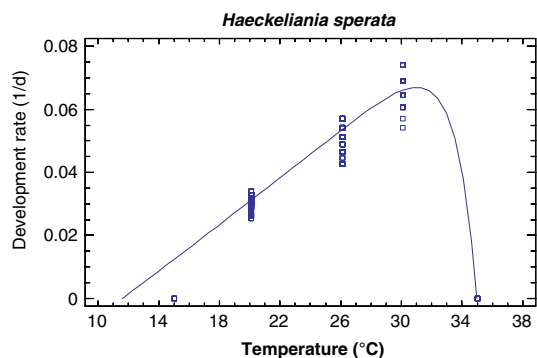
Haeckeliania sperata

The nonlinear regression (Lactin et al. 1995; Logan et al. 1976) fitted to development data resulted: $r(T) = e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\Delta]} - \lambda$; $\rho = 0.0035 \pm 0.0001$; $\Delta = 1.4413 \pm 0.0722$; $\lambda = -1.0412 \pm 0.0008$, estimate \pm asymptotic standard error (Fig. 2). The estimated UDT was $35.0^{\circ}C$, and the MDR occurred at $31.0^{\circ}C$. Development rates observed between 15 and $26^{\circ}C$ were further fit with a linear regression [$r(T) = 0.0036 T - 0.0406$; $R^2 = 94.90\%$; $F = 18911.51$; $df = 1, 1017$; $P < 0.0001$]. The LDT estimated from this equation was $11.3^{\circ}C$. Using this estimate, a thermal constant for development from egg to adult of 279.72 ± 0.54 DD ($n = 1,018$) was calculated.

Discussion

Our regressions indicate that *F. dominica* and *H. sperata* could successfully develop between 9.6 and $30.0^{\circ}C$ and 11.3 and $35.0^{\circ}C$, respectively (LDT and UDT, respectively). However, the LDT estimated for *H. sperata* seems unrealistic as it is located beyond the experimental temperatures that allowed for successful completion of development (Table 2). LDT for *H. sperata* should be around $15^{\circ}C$ and the corresponding thermal

Fig. 2 Development rate (d^{-1}) of *H. sperata* when reared on *D. abbreviatus* plotted against temperature ($^{\circ}C$). Fitted curve: Logan model and modification 2



constant around 188 DD. In the case of *F. dominica*, as we have been able to assess development of the different stages, higher temperatures could be endured provided that they do not coincide with critical stages such as pupation (Table 1). As expected for closely evolved species, such as host-parasitoid assemblages, thermal limits roughly fit within those of the host *D. abbreviatus*, whose LDT is 12°C and UDT 30–32°C (Lapointe 2001).

Extreme ambient temperatures registered in summer and winter are a crucial factor which can dramatically affect parasitoid establishment in classical biological control programs (Goolsby et al. 2005; Llàcer et al. 2006). Consequently, summer and winter temperatures in southern and central Florida where *D. abbreviatus* is distributed can be a key factor that can significantly affect parasitoid development and survival (Ulmer et al. 2006). Ambient temperatures fluctuate around 30°C during the summer in both southern and central areas of Florida, whereas minimum ambient temperatures during January through March in southern Florida fluctuate between 15 and 17°C with mean temperatures of 19–20°C, and between 10 and 13°C with a mean temperature of 15°C in central Florida (Anonymous 2005) (Fig. 3). Depending on how long temperatures stay beyond the estimated development thresholds, these could negatively affect the establishment and success of these tropical biocontrol agents. It should be kept in mind that the eggs of *D. abbreviatus* are concealed between two leaves, and this may offer an extra protection against extreme ambient temperatures not only for the host but also for its parasitoids. A potential advantage of both *F. dominica* and *H. sperata* when compared to other candidates, such as the eulophids *Quadrastichus haitiensis* (Gahan) (Castillo et al. 2006) and *Aprostocetus vaquitarum* Wolcott (Jacas et al. 2005; Ulmer et al. 2006), is their higher tolerance to both minimum and maximum temperatures (Table 3). In fact, *Q. haitiensis* and *A. vaquitarum* have been recovered in southern Florida only (Jacas et al. 2005; Castillo et al. 2006). If *F. dominica* and *H. sperata* are eventually recovered from orchards located at a higher latitude, this would reveal that their thermal plasticity is higher than that of the other parasitoids introduced up till now.

Fidiobia dominica sex ratio was male biased at 15°C whereas it was female-biased at higher temperatures (Table 1). Because primary sex ratio (the sex ratio at oviposition) was the same for all temperatures, the observed adult sex ratio indicates a greater mortality experienced by females at 15°C while immature. Temperature can affect sex ratio of parasitoid wasps, especially under extreme conditions of either hot or cold (King 1987), and differential mortality usually makes females suffer a greater mortality than males (Godfrey 1994). These results are indicative that close to limit zones, *F. dominica* has an

Fig. 3 Mean minimum and mean maximum monthly temperatures at Miami (southeast) and Lake Alfred (central), Florida. Data was obtained from the Southeast Regional Climate Center for Miami WSCMO airport (82.2°W long., 25.6°N lat., 2.3 m alt.) for the period 1948–2004 and Lake Alfred Experimental Station (81.5° W long., 28.1° N, 48.9 m alt.) for the period 1924–2000

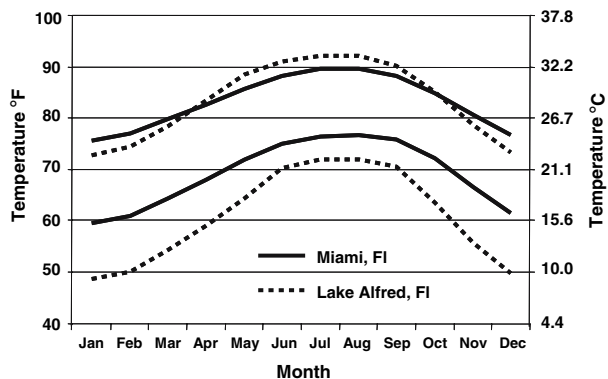


Table 3 Thermal requirements of different egg parasitoids of *D. abbreviatus*

	UTT (°C)	LTT (°C)	Max Dev T (°C)	K (DD)
<i>Fidiobia dominica</i>	30.0	9.6	27.6	293.1
<i>Haekeliana sperata</i>	35.0	11.3*	31.0	279.7*
<i>Quadrastichus haitiensis</i> ^a	33.8	16.0	32.0	200.5
<i>Aprostocetus vaquitarum</i> ^b	33.0	15.8	30.9	494.2

UTT: upper temperature threshold; LTT: lower temperature threshold; Max Dev T: Maximal development temperature; K: thermal constant

*Estimates considered unrealistic because of actual values measured in our experiments

^a Castillo et al. (2006)

^b Ulmer et al. (2006)

extra constraint for its successful establishment that *H. sperata* and other egg parasitoids of *D. abbreviatus* studied so far (Castillo et al. 2006; Ulmer et al. 2006) do not have.

Based on the thermal constants estimated (Table 3), and provided that host eggs were available during the whole season, *F. dominica* would be able to complete 18 generations annually (with a maximum of almost two per month in July and August, and more than one even during the coldest months) in Miami, whereas *H. sperata* would complete from 17 to 18 generations depending on the thermal constant used (with a maximum of two generations per month in July and August, and less than one from November through February). However, host availability during critical periods should not be forgotten. Lapointe et al. (2007) have recently demonstrated that air temperature $\leq 12^{\circ}\text{C}$ is lethal to eggs of *D. abbreviatus*, both those already oviposited and those present in the ovaries prior to oviposition. Such a limitation for the reproduction of *D. abbreviatus* can severely affect the ability of egg parasitoids to establish and successfully control *D. abbreviatus* in areas where winter temperatures fluctuate around the aforementioned threshold. Even if adult parasitoids could endure temperatures below the estimated LDT, the absence of host eggs for prolonged periods of time during winter months in central Florida counties where *D. abbreviatus* occurs could preclude the establishment of these parasitoids. Lapointe et al. (2007) found winter periods of up to 141 d when no egg masses were observed in an orchard located in Fort Pierce ($27^{\circ}26.47'10''\text{N}$ lat, $80^{\circ}19.33'04''\text{W}$ long, 5 m high). Under these circumstances, only the presence of alternative host eggs could allow the introduced parasitoids to reproduce during such periods. There are 11 genera of weevils associated with citrus in Florida and the West Indies (Woodruff 1985), of which at least five species occur in Florida (Knapp 1985). Three of them (the genera *Lachnopus*, *Pachnaeus* and *Compsus*) lay their eggs as *D. abbreviatus* does. However, whether these weevils or other closely related species could be alternative hosts for the imported parasitoids remains unknown and deserves further research. Studies on alternative hosts could help increase the chances of completing a biological control program against *D. abbreviatus*. Additionally, the selection of races or biotypes of these parasitoids from higher elevation areas of the Caribbean Islands could yield specimens with increased cold-tolerance, which could be useful not only in limit zones of Florida, but also in Texas and California, if needed.

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