

Effect of temperature on the life history of *Encarsia bimaculata* (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Hemiptera: Aleyrodidae)

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Abstract. *Encarsia bimaculata* (Heraty & Polaszek) is an abundant parasitoid of *Bemisia tabaci* in southern China. The effects of constant temperatures on a range of life history traits, including development, survival of immatures, longevity and reproduction of adults, were studied in the laboratory. The developmental period from egg to adult ranged from 34.3 ± 0.4 d at 20°C to 8.7 ± 0.6 d at 32°C. A total of 181.4 ± 2.4 degree-days were required to complete development with a lower developmental threshold of 11.6 ± 0.3 °C. The survivorship of *E. bimaculata* from 2nd instar to adult varied from $81.3 \pm 1.7\%$ at 20°C to $91.0 \pm 1.8\%$ at 26°C. Average adult female longevity was 8.4 ± 0.7 d at 20°C and 5.4 ± 0.4 d at 32°C, and daily production of offspring peaked at 29°C with 4.5 offspring per female. The maximum oviposition occurred three days after adult emergence at 23, 26, 29 and 32°C, and four days at 20°C. Total number of offspring produced per female varied from 24.3 ± 2.0 at 32°C to 29.3 ± 2.9 at 20°C. The maximum intrinsic rate of increase (r_m) was 0.2163 ± 0.013 at 29°C, followed by 0.2062 ± 0.022 at 32°C. Results indicate that *E. bimaculata* reaches its maximum biological potential at temperatures ranging from 26°C to 32°C with 29°C being the optimal temperature.

INTRODUCTION

Sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is an important pest of agriculture and horticulture in many parts of the world (Costa et al., 1993; Brown et al., 1995; Wang & Tsai, 1996). The first record of *B. tabaci* in China was in 1949 (Chou, 1949), but it was not considered to be a major pest until the mid 1990s (Ren et al., 2001; Luo et al., 2002; Qiu et al., 2003a). Prior to the mid 1990s, *B. tabaci* in China most likely belonged to indigenous Asian genetic groups (De Barro et al., 2005). The outbreak and increased status of this pest is attributed to the invasion of *B. tabaci* belonging to the Mediterranean/Asia Minor/Africa race, namely *B. tabaci* biotype B (Luo et al., 2002; Qiu et al., 2003a; Wu et al., 2003; De Barro et al., 2005). Thereafter, the B biotype is recorded damaging crops and ornamental plants in more than 25 of China's 34 provinces.

Chemical control is still the key method used in the management of *B. tabaci*, however, this pest can rapidly develop resistance to insecticides and so the sole reliance on insecticides, is unsustainable in the long term (Byrne et al., 2003). Natural enemies, including parasitoids and predators, are regarded as potential agents for use in the classical biological control of this pest (Liu & Stansly, 1996; McAuslane & Nguyen, 1996; Gerling et al., 2001; Ren et al., 2001; Qiu et al., 2005). In China, 19 species of aphelinids are recorded parasitizing *B. tabaci* and of these, *Encarsia bimaculata* (Heraty & Polaszek) appears to be the principle species in southern China, accounting for 32.3% and 33.9% of the parasitism recorded in surveys in southern China between 2000 and 2001 (Qiu et

al., 2004a). However, little is known about this parasitoid and its potential as an effective control agent. Qiu & Ren (2005) investigated the effect of host plants on the development, survival and reproduction of *E. bimaculata*. Here the effect of temperature on development, survival and reproduction of *E. bimaculata* is determined in order to assess the potential of this parasitoid for use in classical and augmentative biological control programmes against the B biotype of *B. tabaci*.

MATERIAL AND METHODS

Host plant

Eggplants, *Solanum melongena* L. var Yuefengzihong are grown individually in 12 cm diameter plastic pots and used in the experiments at the 4–6 leaf stage.

Insect cultures

Bemisia tabaci was originally collected on hibiscus, *Hibiscus rosa-sinensis* L. (Malvaceae) in Teem Plaza, Guangzhou City in 2001, and was identified as B biotype using both RAPD-PCR (De Barro & Driver, 1997) and mitochondrial CO1 (Frohlich et al., 1999). *Encarsia bimaculata* was collected near South China Agricultural University and identified by Jian Huang (Fujian Agriculture & Forestry University, China). Voucher specimens are available from the Laboratory of Biological Control, South China Agricultural University.

Both the whitefly and the parasitoid were maintained on hibiscus in a greenhouse, and a subcolony maintained in rearing cages (60 × 60 × 60 cm) in the laboratory for 10 generations before being used in the experiments. Conditions in the laboratory were 26.0 ± 0.5 °C, 70–80% relative humidity, 14L : 10D photoperiod and a light intensity of 3000 Lux.

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Developmental period and survival of immatures

Approximately 40 pairs of *B. tabaci* adults were released into a leaf-clip cage (3 cm diameter and 1.5 cm high) on the under-surface of either the 3rd or 4th leaf of an eggplant. Adults were allowed to lay eggs for 12 h before being removed. Preliminary studies showed that *E. bimaculata* is able to parasitize all the nymphal stages of *B. tabaci*, but prefers the 3rd and 4th instars (Qiu B.-L., unpubl. data), therefore, the 3rd and early 4th instars were used in experiments.

A newly emerged female and two males of *E. bimaculata* were confined in a petri dish for 4–6 h, and mating was observed at a magnification of 40× using a binocular microscope. Each mated female was then transferred to a leaf-clip cage containing 3rd or early 4th instar *B. tabaci* B biotype nymphs at an average density of 5.38 nymphs/cm² (range 4–11). Females were then left to oviposit for 12 h. From the 4th day post-parasitization, larvae of *E. bimaculata* within the whitefly nymphs were examined daily using a stereomicroscope to observe the parasitoid larvae through the cuticle of the nymph. The number of parasitoid larvae visible inside a nymph (usually in the early second instar) and the time from oviposition to the emergence was measured. The survival of juvenile parasitoids is also noted.

The experiments were carried out at 17°C, 20°C, 23°C, 26°C, 29°C, 32°C and 35°C in separate temperature-humidity controlled incubators (PXY-300Q-A, Shaoguan Keli Experimental Instrument Co., Ltd., Shaoguan, China) at a 70–80% R.H., 14L : 10D day length and 3000 Lux. The ranges of temperatures are those prevailing in South China. Four batches of thirty *E. bimaculata* larvae were examined at each temperature. Those that died during development were not included in the analysis.

Longevity and reproduction of adult females

Mated females were obtained as described above, and introduced into leaf-clip cages as above. Parasitoids were transferred to new clip cages every 24 h and the old leaves were examined daily until the parasitoid larvae were visible in the whitefly nymphs. The longevity and fecundity of each female adult was recorded.

The experiments were carried out at 20°C, 23°C, 26°C, 29°C and 32°C in separate temperature-humidity controlled incubators at a 70–80% R.H., 14L : 10D and 3000 Lux. Four batches of thirty female parasitoids were kept at each temperature.

Data analysis

Differences in developmental times, survival of juveniles, adult longevity and fecundity were compared using analysis of variance (PROC ANOVA, SAS Institute, 2003). Where the differences were significant, means were separated using Student-Newman-Kuel multiple range test at a significant level of $\alpha = 0.05$ (SAS Institute, 2003).

The life table parameters; intrinsic rate of increase (r_m), net reproductive rate (R_0), mean generation time (T), doubling time (DT) and finite rate of increase (λ) were computed according to Birch (1948) using a statistical jackknife technique (Maia et al., 2000). The life table parameters were compared using analysis of variance (PROC ANOVA, SAS Institute, 2003). Means were separated using Student-Newman-Kuel multiple range test at a significant level of $\alpha = 0.05$ (SAS Institute, 2003). The lower developmental threshold temperature (T_b) was estimated by using a weighted linear regression of mean developmental rate against temperature: $v = a + b \times T$, where v is developmental rate, a and b are constants and $T_b = -(a/b)$. Degree-Days (DD) needed for development was calculated as: $DD = (T - T_b) \times D$, where T is treatment temperature (°C), T_b is lower developmental threshold temperature, and D is the mean developmental time in days at temperature T .

RESULTS

Developmental periods and survival of immatures

In all cases, temperature had a significant effect on both development and survival of *E. bimaculata* (Table 1). The developmental time from egg to adult of the parasitoid ranged from 34.3 d at 17°C to 8.7 d at 32°C. Within the range of 17°C to 32°C, developmental time decreased with increase temperature, however, developmental time was more prolonged when temperature exceeded 32°C. There were no significant differences between the developmental times, recorded at temperatures ranging from 29°C to 32°C. For temperatures ranging from 17–35°C, a total of 181.4 ± 2.4 degree-days (DD) were required to complete development with a lower developmental threshold (T_b) at $11.6 \pm 0.3^\circ\text{C}$.

Survival from early second instar to adult emergence differed at the 7 temperatures (Table 1). The percentage survival was lowest at 81.3% at 17°C, and peaked to 91.0% at 26°C. From 17°C to 26°C, survival increased

TABLE 1. Developmental period and percentage survival of immatures of *E. bimaculata* at seven temperatures.

Temperature (°C)	n	Developmental period (d)	Survival (%)
		Egg to adult, mean \pm SE	Second instar to adult, mean \pm SE
17	84	34.3 \pm 0.42 a	81.3 \pm 1.70 b
20	86	22.8 \pm 0.37 b	85.0 \pm 2.17 ab
23	87	15.1 \pm 0.27 c	85.5 \pm 1.08 ab
26	92	12.1 \pm 0.15 d	91.0 \pm 1.84 a
29	84	9.2 \pm 0.22 f	90.3 \pm 2.55 a
32	82	8.7 \pm 0.58 f	84.8 \pm 0.97 ab
35	80	10.3 \pm 0.06 e	83.3 \pm 1.65 b
F		1375.70	14.92
df		6, 588	6, 21
P		< 0.0001	0.0028

n – the total number of individuals in 4 replicates. Within the same column the values with different letters are significantly different at $P < 0.05$.

TABLE 2. Longevity and reproduction of *E. bimaculata* adults at five temperatures.

Temperature (°C)	n	Longevity of female adults (days)		Offspring per female		
		Mean ± SE	Range	Mean ± SE	Range	Daily reproduction
20	84	8.4 ± 0.68 a	5–10	29.3 ± 2.91 a	16–38	3.5
23	84	7.6 ± 0.46 a	5–9	26.8 ± 1.88 ab	17–31	3.5
26	86	6.6 ± 0.42 b	4–8	27.6 ± 2.11ab	15–36	4.2
29	80	5.9 ± 0.27 c	4–7	26.8 ± 1.28 ab	23–33	4.6
32	80	5.4 ± 0.35 c	4–7	24.3 ± 2.02 b	14–33	4.5
<i>F</i>		33.43		130.26		
<i>df</i>		4, 409		4, 409		
<i>P</i>		< 0.0001		< 0.0001		

Within the same column values with different letters are significantly different at $P < 0.05$.

with increasing temperature, however, when the temperature exceeded 29°C, survival declined markedly. Results indicate that temperatures of 26–29°C are optimal for the development of *E. bimaculata*.

Longevity and reproduction of adults

Temperature had a significant effect on both the longevity and reproduction of *E. bimaculata* (Table 2). As expected, longevity decreased as temperature increased with average longevity ranging from 8.4 d (range 5–10) at 20°C to 5.4 d (range 5–9) at 32°C. The maximum adult lifespan was 10 d at 20°C decreasing to 4 d at 26°C, 29°C and 32°C.

The rate of oviposition depended on female age and was strongly related to temperature (Fig. 1). The average number of offspring produced by *E. bimaculata* varied from 29.3 per female at 20°C to 24.3 at 32°C. The maximum number of offspring produced was 38 at 20°C and the lowest was 14 at 32°C. The average daily number of offspring produced per female ranged from 3.5 at 20°C to 4.6 at 29°C. The daily number of offspring produced and the daily survival of females are presented in Fig. 1.

Life table parameters

The effect of temperature on the intrinsic rate of increase (r_m), net reproductive rate (R_0), doubling time (DT), mean generation time (T) and finite rate of increasing (λ) are presented in Table 3. Generation time decreased with increasing temperature, from 29.5 d at 20°C to 11.9 d at 32°C. Net reproduction was maximal at 26°C (18.2 viable females per female). The doubling time decreased from 7.9 d to 3.1 d as temperature increased

from 20°C to 29°C. The finite rate of increase peaked at 29°C (1.24). The maximum intrinsic rate of increase was 0.2163 ± 0.01 at 29°C, followed by 0.2062 ± 0.02 at 32°C (viable females per female). The intrinsic rates of increase at the different temperatures differed significantly ($F = 1944.42$, $df = 4, 15$, $P < 0.0001$).

DISCUSSION

In southern China, surveys have indicated that there are more than 10 species of aphelinids parasitizing *B. tabaci*, with *E. bimaculata* being one of the most abundant (Ren et al., 2001; Qiu et al., 2004a). Since 1993, Enkegaard (1993), De Barro et al. (2000), Xu et al. (2003), Antony et al. (2004), Qiu et al. (2004b) have recorded the life history parameters of *Encarsia* spp. at different temperatures. The use of constant temperatures facilitated the comparison of the performance of these *Encarsia* parasitoids.

Developmental time

Developmental times of *E. bimaculata* varied from 9.2 d to 15.1 d across the temperature range 23°C to 29°C when reared on host feeding on eggplants. Over a similar temperature range (22°C to 30°C), the developmental time of *E. bimaculata* (Bundaberg population) (De Barro et al., 2000) ranged from 16–18 d when reared on host feeding on hibiscus. Antony et al. (2004) report that the developmental periods for male and female *E. bimaculata* (Indian population), parasitising *B. tabaci* on cassava at 25–30°C, averaged 12.7 d and 14.5 d for females and males, respectively. Within the same genus, Xu et al. (2003) found that *Encarsia formosa* require 20.2 d, 14.5 d

TABLE 3. Life table parameters for *E. bimaculata* at five temperatures (95% CI).

Temperature (°C)	Generation time (T) (days)	Net reproduction rate (R_0)	Doubling time (DT) (days)	Finite rate of increase (λ)	Intrinsic rate of increase (r_m)*
20	29.50	11.09	7.87	1.09	0.0816 ± 0.013 e
23	22.04	16.31	5.28	1.14	0.1267 ± 0.009 d
26	15.30	18.21	3.52	1.21	0.1892 ± 0.016 c
29	11.92	13.15	3.13	1.24	0.2163 ± 0.010 a
32	12.85	14.16	3.19	1.23	0.2062 ± 0.022 b

* Within the column of r_m , the values with different letters are significantly different at $P < 0.05$ ($F = 1944.42$, $df = 4, 15$, $P < 0.0001$).

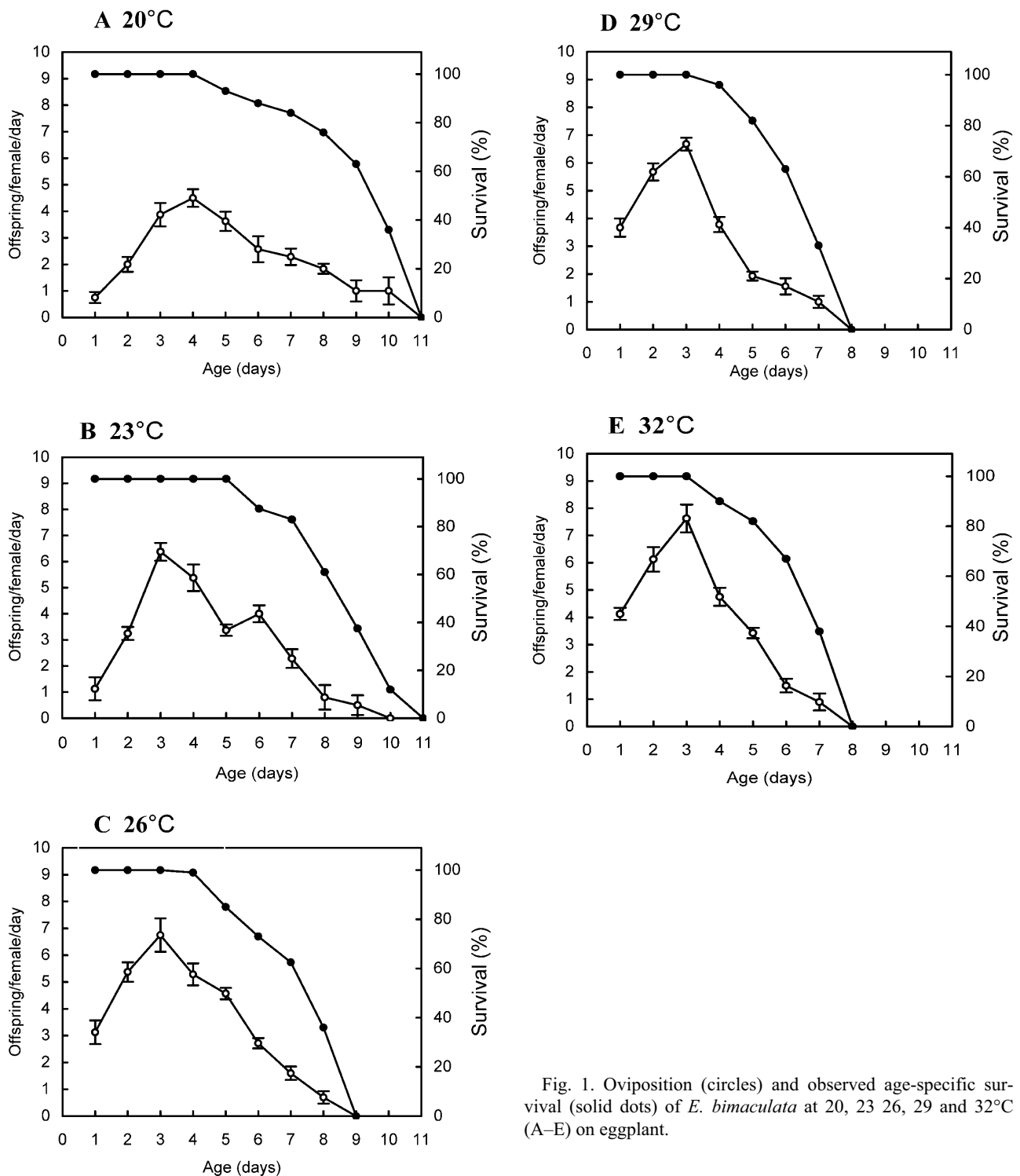


Fig. 1. Oviposition (circles) and observed age-specific survival (solid dots) of *E. bimaculata* at 20, 23, 26, 29 and 32°C (A–E) on eggplant.

and 12.9 d for development at 20°C, 25°C and 30°C, respectively, while Qiu et al. (2004b) report that the development period of *E. formosa* at 32°C is about 14 d. While temperature clearly influences the rate of development, the above differences are also likely to be affected by differences in the genetic stock from which the parasitoids were obtained and the host plant of the whitefly host.

Longevity of adult

The longevity of *E. bimaculata* at different temperatures has not been previously reported. However, there are several such studies on *E. formosa* parasitising *B. tabaci* (Bethke et al., 1991; Enkegaard, 1993; Xu et al., 2003). In these studies, the adult longevity of *E. formosa* is reported to be 4.8 d at 25.4°C (Bethke et al., 1991), 15.2 d at 22°C, 9.2 d at 28°C (Enkegaard, 1993), 17.7 d at 25°C and 13.6 d at 30°C (Xu et al., 2003). In the present study, the longevity of *E. bimaculata* was 7.6 d at 23°C

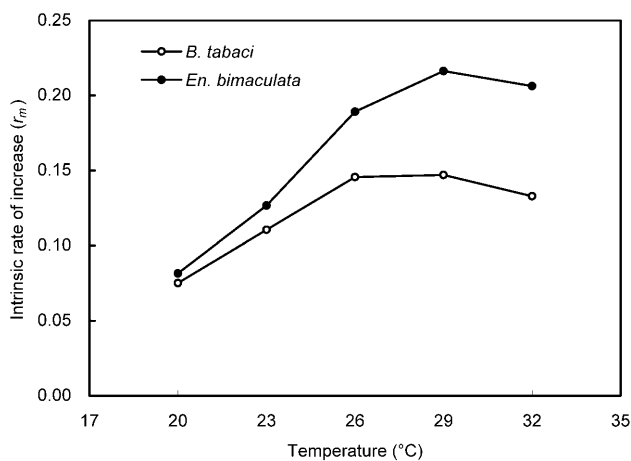


Fig. 2. Intrinsic rate of increase (r_m) of *E. bimaculata* (solid dots) and *B. tabaci* B biotype (circles) on eggplant at five constant temperatures. The data for *B. tabaci* is taken from Qiu et al. (2003).

and 5.9 d at 29°C, which is shorter than that reported for *E. formosa*.

Reproduction

De Barro et al. (2000) studied the mean daily and total number of ovipositions made by *E. bimaculata* over a 10-day period on five host plants at 22–30°C. The mean daily oviposition ranged from 1.7 on soybean to 3.9 on hibiscus with an average of 2.9, whereas the average daily parasitization in our study on eggplant ranged from 3.5 at 20°C to 4.6 at 29°C. Records of *E. bimaculata* on rockmelon and hibiscus at 22–30°C (De Barro et al., 2000) were closer to the rate observed in our study over the same temperature range. The oviposition of *E. bimaculata* peaked on day 3 when parasitizing *B. tabaci* on rockmelon, cotton, tomato, soybean and hibiscus (De Barro et al., 2000), which is as the result reported here at 23, 26, 29 and 32°C. In De Barro et al. (2000) the total number of nymphs parasitized was 11.3 nymphs on soybean, 16.3 on tomato, 26.0 on rockmelon, and 27.8 and 29.5 on hibiscus and cotton, respectively. In our study, the total number ranged from 24.3 nymphs at 32°C to 29.3 at 20°C, which is higher than that reported on soybean and tomato, but similar to rockmelon, hibiscus and cotton. In contrast Xu et al. (2003) observed fecundities for *E. formosa* of 136.7, 132.0 and 124.0 eggs at 20, 25 and 30°C, respectively, which are much higher than those for *E. bimaculata* reported by both our and De Barro et al. (2000).

Comparison of life table parameters of parasitoid and host

The r_m values for *E. bimaculata* at five constant temperatures ranged from 0.0893 at 20°C to 0.2421 at 29°C, while that of *B. tabaci* B biotype at the same temperatures varied from 0.0751 at 20°C to 0.1470 at 29°C (Fig. 2) (Qiu et al., 2003b). This along with the values for R_0 , T and λ indicate that *E. bimaculata* is better adapted to high temperatures than *B. tabaci*. This suggests that within the

range of 20–32°C, and especially at 26–32°C, *E. bimaculata* could intrinsically control *B. tabaci* B biotype.

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