Title: The effects of temperature on the development, fecundity and mortality of *Eretmocerus warrae*: Is *E. warrae* better adapted to high temperatures than *Encarsia formosa*?

Running Title: Effects of temperature on *Eretmocerus warrae* and *Encarsia formosa*

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Abstract

BACKGROUND

Eretmocerus warrae (Hymenoptera: Aphelinidae) is a parasitoid of the greenhouse whitefly, *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae). Here, we compare its potential as a biological control agent at high temperatures to that of *Encarsia formosa* (Hymenoptera: Aphelinidae), a wasp which is widely sold for control of *T. vaporariorum*.

RESULTS

E. warrae attained the highest estimated developmental rate at 31.4 °C and the maximum oviposition rate at 30.5 °C. Developmental times of *E. warrae* at fluctuating temperatures that simulate night-day patterns were similar to those predicted based on constant

temperatures. Above the optimum temperature, *E. warrae* tolerated higher constant temperatures than *En. formosa* during development and as adults. Using a ramping temperature approach, the critical thermal maxima for adult *E. warrae* was significantly higher than that of adult *En. formosa*.

CONCLUSION

E. warrae is better adapted to high temperatures than *En. formosa*, and could therefore be a complementary or superior biological control agent during summer months in hot regions.

Key Words:

Trialeurodes vaporariorum; critical thermal maximum; ramping temperature; survival; fluctuating temperature

1. INTRODUCTION

Greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae), attacks an extensive range of ornamental plants and vegetables, and causes severe damage to greenhouse crops when present at high densities.[1] Although insecticides can suppress this pest, resistance of greenhouse whitefly to insecticides has been demonstrated and biological control is widely used. Among species of biological control agents, the release of *En. formosa* has received much attention in the biological control of greenhouse whitefly.[2] It has been one of the most widely used and effective parasitoids in control of whiteflies in greenhouses in many parts of the world since the 1920s.[3] However, there are some weaknesses that can reduce the efficacy of *En. formosa* in biological control. For instance, greenhouse whitefly colonies still grow in the hot summer when *En. formosa*'s activity and

population growth are decreased by extreme temperatures, and thus it cannot control this pest effectively at high temperatures.[4] Species that have a broader tolerance for extreme temperatures are needed to replace or complement *En. formosa.*

Eretmocerus warrae (Nauman & Schmidt) (Hymenoptera: Aphelinidae) is a parasitoid of the greenhouse whitefly that is suspected to be effective as a biological agent.[5] The solitary parasitoid *E. warrae* was first found in New Zealand in 1997,[6] and studied in Australia by De Barro et al., [7] who presented the morphological and molecular characteristics of this wasp. Because of its potential in suppressing greenhouse whitefly, *E. warrae* is being reared for release in commercial greenhouses in Australia.[8] Observations suggest that *E. warrae* actively parasitizes greenhouse whitefly at higher temperatures than *Encarsia formosa* (Gahan) (Hymenoptera: Aphelinidae) (James Altmann, personal communication). If this proves to be true, then *E. warrae* should be a complementary biological control agent to *En. formosa*, and might be a better control agent when the temperature is high during summer. This study was carried out to study the effects of temperature on the biology of *E. warrae* and determine whether it is able to tolerate higher temperatures than *En. formosa*.

Temperature is a key environmental factor that affects all aspects of arthropod life, from physiology to behavioural patterns.[9] Therefore, the effect of temperature on development, longevity and behaviour of *E. warrae* is significant for its utilization in greenhouses. The development of insects shows a non-linear response to temperature, with the highest developmental rate achieved at an intermediate optimum temperature. Basic parameters, such as lower developmental threshold temperature, developmental rates under different temperature conditions and critical lethal maxima are needed to predict the generation time, which affects the effectiveness of parasitoid populations. The determination of these parameters should enable an advanced release strategy to be formulated in consideration of expected temperature conditions in greenhouses. The effects of fluctuating temperatures on

E. warrae need to be studied because daily fluctuations in temperature are inherent in the operation of greenhouses.

For biological control, the upper threshold temperatures may be more critical than the optimum temperature.[10] When the temperature exceeds the maximum, this can cause death or irreversible injury, or severely limit development and behaviour.[10,11] Insects may also terminate diapause when the temperature is extreme.[12] Therefore methods to estimate the upper lethal threshold are valuable in understanding a species' response to temperature. The dynamic method for estimating upper lethal temperatures uses ramping temperatures to assess the critical upper limit.[13] It is widely used and thought to be more ecologically-relevant than the static method, which uses a range of fixed constant temperatures to estimate the upper lethal temperature. [13]

We conducted experiments to assess the influence of constant and fluctuating temperatures on the development, mortality and oviposition of *E. warrae*. Furthermore, to investigate the potential of *E. warrae* as a complementary biological control agent of *En. formosa* in greenhouses at high temperatures, we compared the developmental rate and survival of *E. warrae* and *En. formosa* at a range of high temperatures. Both constant temperature and ramping temperatures were used. These results will facilitate rearing and effective deployment of *E. warrae* in greenhouses.

2. MATERIALS AND METHODS

2.1. Rearing parasitoids and host

Greenhouse whiteflies were collected from eggplant, *Solanum melongena* L. (Solanaceae), in the greenhouses at the Waite Campus of The University of Adelaide and used to initiate a culture. Tobacco, *Nicotiana tabacum* L. (Solanaceae), plants with at least

five fully expanded leaves and approximately 30 cm high were used to rear the whitefly culture because they can support high densities of these insects. A greenhouse whitefly culture was kept at 26 °C, 40 – 80 % RH and a photoperiod 14 L: 10D.

Pupae of *E. warrae* and *En. formosa* were provided by Biological Services, Loxton, South Australia. A breeding culture of the parasitoids was set up on greenhouse whiteflies feeding on tomato plants, *Solanum lycopersicum* L. (Solanaceae), at 26 °C. Pupae of the two species of parasitoids were harvested from the breeding culture and kept in two separate incubators at 8 °C, 70 – 80 % RH to arrest development. For each species, when adult parasitoids were needed, pupae were moved from 8°C at 20:00 h to another incubator which was set at 26 °C to allow them to emerge. Most adults emerged during the morning when experiments commenced. Adults were kept in cages and honey drops were provided as food.

Six to seven week old tomato plants were used in experiments as a host plant for greenhouse whitefly. The tomato plants had six fully expanded leaves and were approximately 50 cm high. The cultivar '*Improved Appolo*' was used in moderate temperature conditions (15 – 36 °C) whereas '*Summerstar*' was used at higher temperatures (30 - 37.5 °C) because it can better withstand temperatures up to 37.5 °C.

Second instar *T. vaporariorum* were provided as hosts in experiments. Cohorts of 2nd instar nymphs were obtained by exposing tomato plants to adult whiteflies for six hours, and then removing the adults first by blowing them off with a cool hair-dryer and then removing the remaining adults with an aspirator. These cohorts were held in incubators at 26 °C, 70 – 80 % RH until they reached the 2nd instar. If necessary, other stages of nymphs were removed with a pin before experiments.

2.2. Experimental materials

Temperature experiments were conducted in five incubators (Adelab Scientific, Thebarton, South Australia, Model 1390D) that were calibrated to means within 0.1 °C of set temperatures with a precison thermometer (E-MIL, H. J. Elliott Ltd, Treforest, U.K.) and had measured variation of ± 0.3 °C. The rearing temperatures were set according to the experiments and the photoperiod was 14L : 10D.

Clip cages were used to confine insects on tomato leaves.[14] They were made of two rings of 12 mm thickness of polyethylene foam that had inside and outside dimensions of 40 mm and 55 mm, respectively, which were held together over a leaf with wire staples pushed into the edges. There was a transparent cellulose acetate sheet on the bottom of each cage which allowed wasps to be observed and fine organza on top for aeration. An aspirator made of plastic tubing was used to handle wasps. Honey drops were placed on the organza of clip cages as food for *E. warrae*.

2.3. Effects of temperature on the developmental rate of *E. warrae*

To investigate the effects of constant temperatures on the development of *E. warrae*, three clip cages containing a minimum of 100 2nd instar greenhouse whiteflies were attached to selected leaves of each of five tomato plants.. The plants were transferred to experimental incubators that were set at 15, 20, 25, 30 and 33 °C, 70 – 80 % RH. The whitefly nymphs were exposed to newly-emerged adult *E. warrae* for six hours, after which the adults were removed from the clip cages using an aspirator. In the temperature range 15 - 33 °C, the wasp numbers within each clip cage were 13, 4, 3, 2 and 2, respectively. Greater numbers of wasps were used at lower temperatures to compensate for their lower activity levels. The parasitised greenhouse whitefly nymphs were kept in the clip cages, and the emergence of *E. warrae* was monitored daily using a hand lens. There were four replicate plants at each temperature.

The Briere model was used to analyse the developmental rate of *E. warrae*.[10] It is described as

$$R(T) = \begin{cases} 0, \text{ if } T \leq T_0 \\ aT(T - T_0)(T_L - T)^{\frac{1}{m}}, \text{ if } T_0 \leq T \leq T_L \\ 0, \text{ if } T \geq T_L \end{cases} \quad (1)$$

where R is the rate of development, T is the temperature, T_L is the upper threshold temperature, T_0 is the lower threshold temperature, and a and m are empirical constants.

This model has advantages compared to other non-linear models.[15-17] It has few parameters, is biologically descriptive and incorporates both high and low threshold temperatures. Unlike a degree-day model which does not work for the nonlinear relationship between developmental rate and temperature at extreme low and high temperatures, this model fits the broad non-linear relationship across all temperatures.[10] The lower (T_0) and upper (T_L) temperature threshold parameters have biological meaning. The model of Briere et al. has a form that can potentially fit the relationship between temperature and other biological rates.[10] It was also used to evaluate the relationship between temperature and oviposition rate.

The effects of temperature on the developmental rate of *E. warrae* were analysed using non-linear regression in R version 3.2.0 (2015-04-16) to estimate the parameters of the model.[10] Mean developmental rates from each replicate were used as data to balance the analysis.

2.4. Effects of temperature on the oviposition activity of *E. warrae*

The influence of temperature on the oviposition avitivity of *E. warrae* was assessed at 15, 20, 25, 30 and 33 °C, 70 – 80 % RH. Before an experiment, wasps were kept at 25 °C. Each

159 adult *E. warrae* was exposed to 2nd instar greenhouse whitefly for two hours to become
160 experienced in host searching. The wasps were then separated from hosts for one day. This
161 procedure ensured that *E. warrae* would lay eggs quickly when hosts were available. Tomato
162 leaves infested with 2nd instar greenhouse whitefly were placed into the incubators one hour
163 before the experiment. The greenhouse whitefly infested leaves were covered by clip cages,
164 making sure there was an excess of whitefly nymphs in each cage. Four experienced adult *E.*
165 *warrae* were released into each clip cage at the experimental temperature. The wasps were
166 removed from the cages after three hours to ensure that the availability of unparasitised hosts
167 was not limiting behaviour. Because *E. warrae* lays eggs under the ventral part of nymphs, all
168 the nymphs were turned over using a dissecting needle and the number of eggs laid was
169 recorded. Observations at each temperature were replicated four times. The analysis of the
170 effect of temperature on oviposition rate of *E. warrae* was the same as that of experiment 2.3.
171 There were four replicates at each temperature.

172 2.5. The effects of fluctuating temperature on the developmental times of *E. warrae*
173 To investigate whether the development of *E. warrae* under fluctuating temperature
174 conditions differed from that at constant temperatures, the same methods were used as in
175 experiment 2.3, except developing wasps were exposed to two fluctuating temperature
176 regimes. The temperatures were 33 °C in light and 26 °C in dark in the high fluctuating
177 temperature regime, and 25 °C in light and 15 °C in dark in the low fluctuating temperature
178 regime (70 – 80 % RH). The photoperiod was 14L: 10D. The numbers of adult *E. warrae*
179 that parasitized the nymphs were two and four in the high and low fluctuating temperature
180 regimes, according to the activity of the wasps. The developmental times of the parasitoids
181 from egg to adult were recorded and compared to development that was predicted based on
182 development at constant temperatures from the results of experiment 2.3. This experiment
183 had four replicates.

184 2.6. The effects of high temperature on emergence and development of greenhouse
185 whiteflies, *E. warrae* and *En. formosa*

186 The survival of greenhouse whitefly under the high temperature conditions was
187 investigated at 30, 33, 34.5, 36 and 37.5 °C, respectively (70 – 80 % RH). The effects of the
188 same temperatures on the development and survival of *E. warrae* and *En. Formosa* were also
189 assessed. The number of 2nd instar nymphs of greenhouse whiteflies in each clip cage at each
190 temperature was 100. Excessive numbers of nymphs were removed from the leaf with a pin.
191 The numbers of parasitoids of each species released into clip cages were 6, 6, 9, 18 and 36 at
192 temperatures 30, 33, 34.5, 36 and 37.5, respectively. The developmental times of parasitoids
193 and the numbers of adults of each species that emerged were recorded. This experiment was
194 replicated four times. Differences in developmental times between parasitoid species at each
195 temperature were analysed using analysis of variance with replicates treated as blocks, except
196 at 34.5 °C where a paired *t*-test was used due to no development by *En. formosa*.
197 Differences in numbers of parasitoids that emerged at each temperature were analysed with
198 paired *t*-tests by temperature. Statistical comparisions between temperatures were not
199 possible due to the differing numbers of adults that were used to initiate the experiment.

200 2.7. The mortality of adult *E. warrae* and *En. formosa* at constant high temperatures

201 The effects of constant high temperature on the mortality of adult *E. warrae* and *En.*
202 *formosa* were investigated. Adult *E. warrae* and *En. formosa* were placed into glass vials (18
203 mm diam x 50 mm) that had fine stainless steel mesh melted over a 10 mm hole in the plastic
204 lid to provide aeration. The vials rested in close-fitting semi-circular grooves in a dense
205 wooden block (12.5 × 10 × 2.5 cm^3) that had been heated in an incubator to 36 °C or 37.5 °C,
206 70 – 80 % RH, which, according to the results of experiment 2.7, were stressful temperatures
207 for both wasp species. The wooden block was painted white and served as a thermal ballast to
208 maintain a constant temperature inside the vials during brief periods of observation when the

vials were removed from incubators. Pure honey and water were provided on a cotton dental wick to ensure that the wasps did not die from starvation or dehydration. There were 10 wasps in each vial and five replicates at each temperature. The number of dead wasps was recorded every three hours until all wasps died. The time of death was assumed to be the midpoint between observations. The proportional hazards survival regression (Statistix version 10.0, Analytical Software, Tallahassee, Florida, USA) was used to analyse of the survival rate of the parasitoids.

2.9. The critical thermal maxima of adult *E. warrae* and *En. formosa* under ramping temperature conditions

The critical thermal maxima of adult *E. warrae* and *En. formosa* were assessed using the ramping temperature method.[18] A water bath was used for this test and a precision thermometer (E-MIL, H. J. Elliott Ltd, Treforest, U.K.) was used to measure the temperature. Starting at 26 °C, temperatures were increased by 1°C every two minutes in which the temperature increased gradually in the first minute and kept constant in the second minute. Temperatures were controlled at $\pm$0.1 °C. *E. warrae* and *En. formosa* were put into two separate small glass vials with closed lids. A shelf was made of iron wire to fix the vial in the water bath. The vials were fixed in the shelf and they were easy to take out for quick observation (<10 s). The shelf and vials were totally submerged into the water bath during the experiment. A cotton wick saturated with 10 % honey solution was placed in each vial as a water and food source. Ten one-day-old wasps were placed into each vial and this experiment was replicated eight times. The number of dead wasps was recorded at the end of each constant temperature exposure. Logistic regression (Statistix 10.0) was used to estimate the critical thermal maxima of *E. warrae* and *En. formosa*, which was the temperature at which 50% of adults died. In all cases, parameter estimates are given as mean ± standard error.

3. RESULTS

3.1. Effects of temperature on the developmental rate of *E. warrae*

The developmental rate of *E. warrae* increased as the temperature rose from 15 °C to 30 °C (Fig. 1). No development was completed at 36 °C, and this temperature was excluded from the nonlinear regression analysis to fit the Briere model. The estimated optimum temperature for the development of *E. warrae* was 31.4 °C and all parasitoids are predicted to die when the temperature reaches 35.6 ± 1.1 °C. The lower threshold temperature of *E. warrae* was 9.7 ± 0.8 °C; and the parameter "a" in Briere model was $6.41e^{-5} \pm 1.18e^{-5}$ and "m" was 3.13 ± 0.82. At 15 °C, it took more than two months for *E. warrae* to develop from egg to adult, which is around four times longer than the developmental time at 30 °C.

3.2. Effects of temperature on oviposition of *E. warrae*

The oviposition rate of *E. warrae* increased as the temperature rose from 15 °C to 30 °C (Fig. 2). No eggs were laid at 35 °C, and this temperature was excluded from the nonlinear regression analysis to fit the Briere model. The estimated optimum temperature for oviposition was 30.5 °C.The estimated lower critical temperature threshold for oviposition by *E. warrae* was 13.7 ± 0.8 °C and the upper critical threshold was estimated at 34.9 ± 1.4 °C. The empirical model parameters "a" and "m" in the model were estimated to be 0.00324 ± 0.00083 and 2.43 ± 0.95.

3.3. The effects of fluctuating temperatures on developmental rate of *E. warrae*

The observed developmental times did not differ significantly from those predicted on the basis of the calculated means of fluctuating day and night temperatures (high temperatures: $t = 0.633$, $df = 3$, $P = 0.57$; low temperatures: $t = 0.917$, $df = 3$, $P = 0.427$; Table 1).

3.4. The effects of high temperature on on emergence and development of greenhouse whiteflies, *E. warrae* and *En. formosa*

The numbers of greenhouse whiteflies that emerged decreased markedly when the temperature increased from 30 °C to 34.5 °C (Table 2). No successful development was observed at 36 °C and 37.5 °C, while less than 5 % of adults on average emerged at 34.5 °C, which is roughly 10 times fewer than at 30 °C.

Constant high temperatures had a greater negative influence on *En. formosa* than *E. warrae* (Table 2). The numbers of adult *E. warrae* and *En. formosa* that emerged did not differ at 30 °C and 33 °C. Some adult *E. warrae* emerged at 34.5 °C but no *En. formosa* did. The developmental times of both parasitoids increased at the highest recorded temperature in which they survived.

3.6. The mortality of adult *E. warrae* and *En. formosa* at high temperatures

Proportional hazards analysis indicated that survival of adult parasitoids at constant high temperatures differed between species ($Z = 4.94$, $P < 10^{-4}$) and temperatures ($Z = 2.20$, $P = 0.028$). Adult *E. warrae* survived 5.4 h longer than *En. formosa* at constant 36 °C and 3.7 h longer at 37.5 °C (Fig. 3).

Logistic regression indicated that ramping temperatures affected the species differently ($Z = 5.787$, $P < 10^{-8}$; Fig. 4). The estimated critical thermal maximum temperature for *E. warrae* is 42.6°C and for *En. formosa* is at 41.8 °C. One *E. warrae* in replicate three died when the temperature was 35 °C; this single wasp was discarded from the data because it was a statistical outlier.

4. DISCUSSION

The developmental rate of *E. warrae* in the range of 15 to 30 °C is broadly similar to *En. formosa*, *Eretmocerus mundus* (Mercet) and *Eretmocerus eremicus* (Rose) (Hymenoptera: Aphelinidae), which are widely used in biological control (Fig. 1).[19] Its development at high temperatures is constrained by the development of its host, which in our experiments also did not occur at 36 °C (Table 2). The maximum rate of development of *E. warrae* is predicted at 31.4 °C, which is commonly exceeded during the summer months. The high developmental rate of *E. warrae* at high temperatures indicates the potential of using *E. warrae* and *En. formosa* in combination, as *E. warrae* should suppress greenhouse whitefly more effectively during the hot summer while *En. formosa* is known to control whiteflies at lower temperatures[3]. This is analogous to the complementary relationship between *En. formosa* and *E. eremicus*, which are released for control of *T. vaporariorum* and *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) in European greenhouses.[19] The predicted relationship between temperature and development is useful for optimising methods for the mass rearing and deplolyment of this parasitoid. There is limited research on the effects fluctuating temperatue on parasitoids, but fluctuating temperatures are normal in production systems. When *E. warrae* was reared in fluctuating temperatures, its developmental times were virtually the same as those predicted based on rearing at constant temperatures with the same mean (Table 1). This suggests that the model of the developmental rate based on development at constant temperatures can be applied to predict the approximate timing of developmental under moderate fluctuating temperatures in greenhouses.

E. warrae has a relatively high oviposition rate even when the temperature is 33 °C (Fig. 2), which should facilitate its controlling influence on greenhouse whitefly under such host conditions. The effects of temperature on oviposition show a similar response to developmental rate, but oviposition is predicted to occur over a more limited temperature

range. *En. formosa* is reported to mature 8-10 eggs per day, which is equivalent to the maximum number laid by *E. warrae* in 3 h at 30.5 °C.[20] However, *E. warrae* exhibits deterotoky, with rare production of males in culture, so it is likely to have much greater reproductive potential than *En. formosa*.

The development of greenhouse whitefly was adversely affected by relatively high temperatures and this was reflected in the development and survival of the two parasitoids (Table 2). The impact of temperatures above 30 °C on survival of the host constrains the potential development of its parasitoids, which was reflected in their observed developmental rates and survival. The effects of high temperature were evident at a lower temperature for *En. formosa* than for *E. warrae*. As *E. warrae* completed development at the same high temperatures as its host, it has the potential to persist in greenhouses as long as immature greenhouse whiteflies are present.

Adult *E.warrae* survived both constant and ramping high temperatures better than *En. formosa* (Figures 3 and 4). Although the differences between the species are small, they may still be significant in greenhouses where summer temperatures are extreme. Extreme high temperatures typically occur in the afternoon hours. The evaporative systems that are used to cool greenhouses have a maximum potential temperature reduction in the order of 12 °C, which limit maximum temperatures.[21] However, extreme temperatures do not last long during a day and may not occur on many days of the year. Hence a species that can better withstand high temperatures for short periods could be potentially better in applied biological control programs in regions with high temperatures during summer months. This is consistent with the observation that *E. warrae* can be found naturally parasitising greenhouse whiteflies in greenhouses in the South Australian summer.

5. CONCLUSION

Our results indicate that *E. warrae* should be a complementary biological control agent to *En. formosa* in greenhouses when the summer temperatures are high. At high temperatures, *E. warrae* had a higher survival and emergence of adults than *En. formosa*, and this highlights its potential as a biological control agent. *E. warrae* could be used alone or in combination with *En. formosa*, notably in hot regions. This research should enable farmers to use *E. warrae* as part of a pest management program to achieve more effective control of greenhouse whitefly.

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Table 1. The developmental time (mean ± SE) of *E. warrae* at two fluctuating temperature regimes compared to model predictions. The predicted developmental time was obtained using the Briere model fitted to constant temperature data (see Fig. 1).

Temperature regime (°C)		**Developmental time (days)**	
14 h Light	**10 h Dark**	**Observed**	**Predicted**
33.0	26.0	14.98 ± 0.12	14.90
25.0	15.0	27.93 ± 0.45	28.34

Table 2. Adult emergence numbers and developmental times (mean ± SE) of *E. warrae* and *En. formosa* at a range of high temperatures. One hundred *T. vaporariorum* were present at the start of each trial. The effect of high temperatures on adult emergence of *T. vaporariorum* was tested in the absence of parasitoids.

Temperature (°C)	**No. of *T. vaporariorum* emerged**	**No. of *E. warrae* emerged /female**	**No. of *En. formosa* emerged /female**	**Developmental time of *E. warrae* (day)**	**Developmental time of *En. formosa* (day)**
30.0	44.3 ± 2.8	4.1 ± 0.4	4.3 ± 0.1 *ns*	14.52 ± 0.11	14.33 ± 0.11 *ns*
33.0	17.3 ± 1.5	2.0 ± 0.1	1.4 ± 0.1 *ns*	14.36 ± 0.14	15.65 ± 0.21 ***
34.5	4.5 ± 1.0	0.5 ± 0.1	0 *	15.46 ± 0.55	0 ***
36.0	0	0	0	0	0
37.5	0	0	0	0	0

Comparisions between parasitoid species: * $P < 0.05$, *** $P < 0.001$

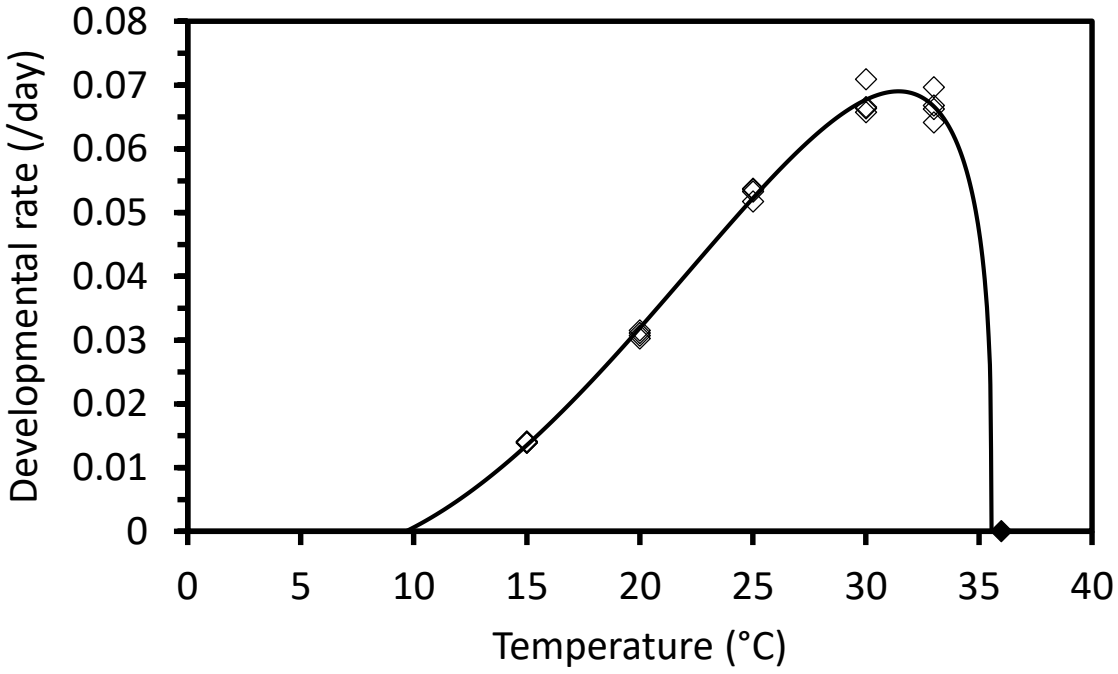
FIGURE LEGENDS

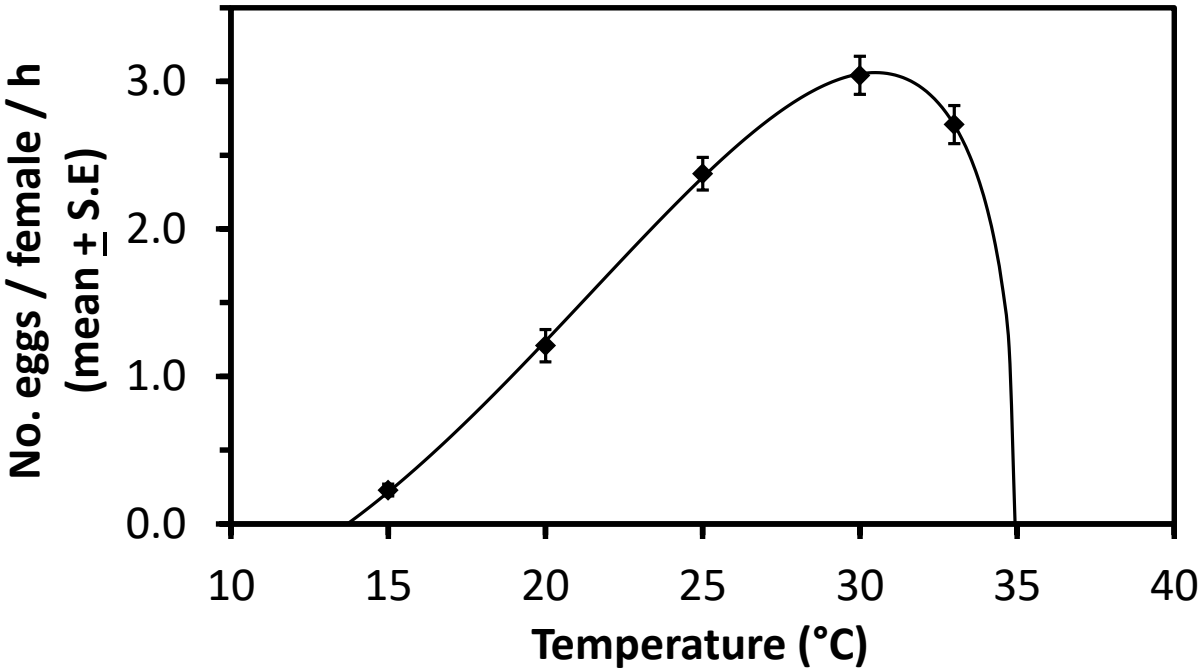
Figure 1. Temperature-dependent developmental rate (±SD) of *Eretmocerus warrae*. In the Briere model, a = 0.00006, m = 3.07, T_0 = 9.62, T_L = 35.63. Where no error bar is visible, the standard deviations were ≤ 0.001 /day. 550 observations in total.

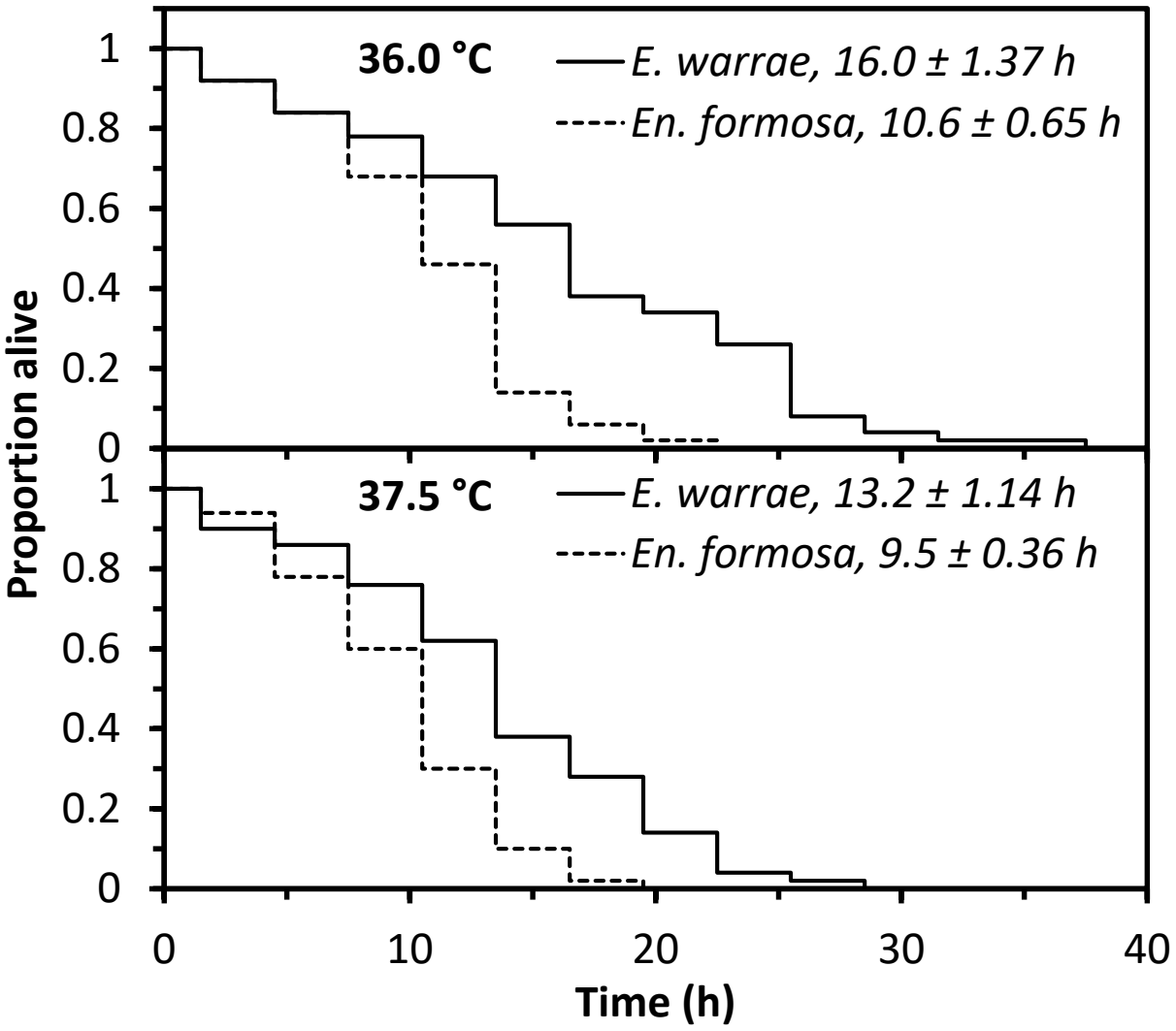
Figure 2. Temperature-dependent fecundity (±SD) of *Eretmocerus warrae*. In the Briere model, a = 0.004, m = 2.43, T_0 = 13.70, T_L = 34.94. The standard deviation was 0.96 at 15 °C. 459 observations in total.

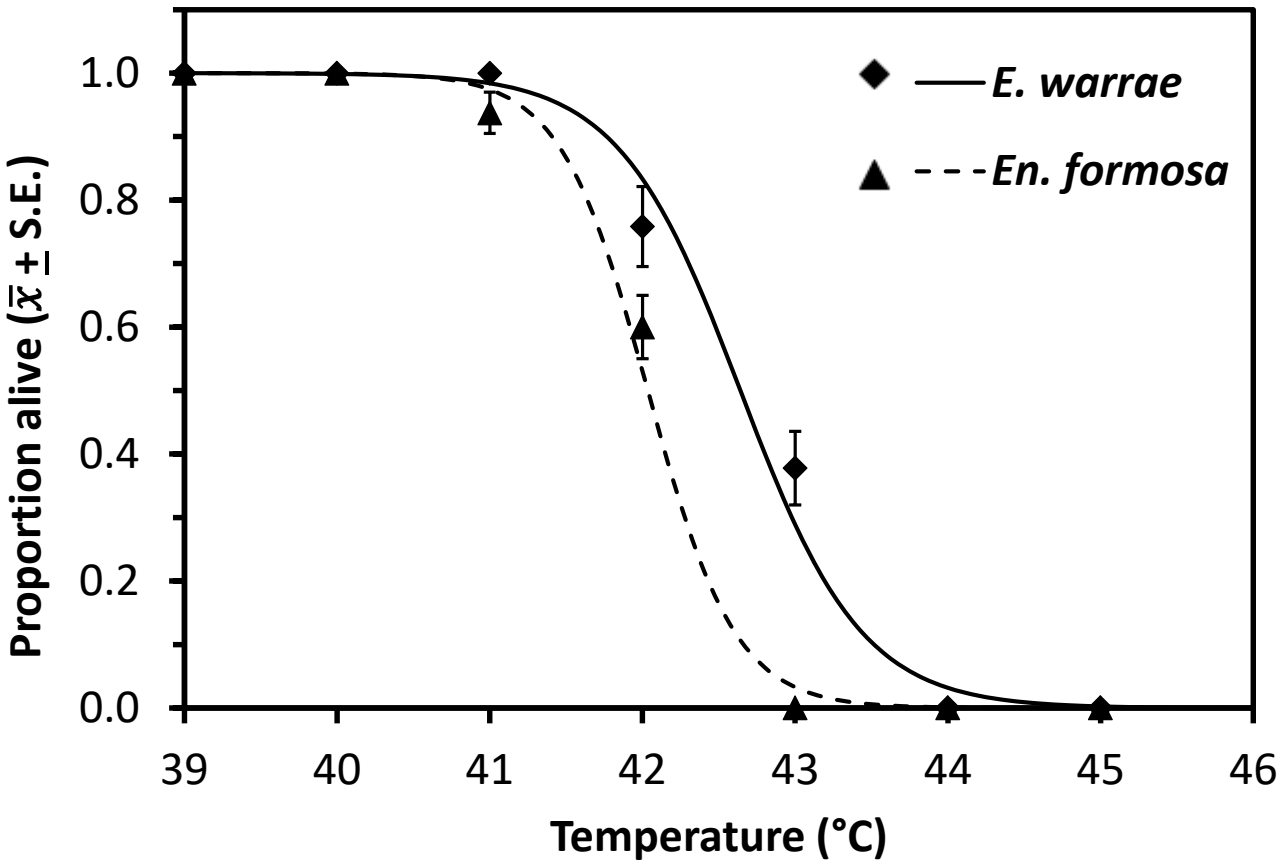
Figure 3. Survival analysis of *Eretmocerus warrae* and *Encarsia formosa* at 36 and 37.5 °C. Dotted line is the survival rate of *En. formosa* at 36 °C, dash- and dotted line is that of *E. warrae* at 36 °C, dashed line is *En. formosa* at 37.5 °C and solid line is *E. warrae* at 37.5 °C. (χ^2=28.78, df = 2, P < 0.001)

Figure 4. Survival of *Eretmocerus warrae* and *Encarsia formosa* using ramping temperature. Curves fitted by logistic regression: a) Survival rate of *E. warrae*, the constant is 115.76, deviance 188.52, P = 0.049, df = 158; b) Survival rate of *E. formosa*, the constant is 155.98, deviance 143.99, P = 0.71, df = 154.


0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
Developmental rate (/day)
0
5
10
15
20
25
30
35
40
Temperature (°C)


No. eggs / female / h
(mean ± S.E)
3.0
2.0
1.0
0.0
10
15
20
25
30
35
40
Temperature (°C)


36.0 °C
E. warrae, 16.0 ± 1.37 h
En. formosa, 10.6 ± 0.65 h
37.5 °C
E. warrae, 13.2 ± 1.14 h
En. formosa, 9.5 ± 0.36 h
Proportion alive
Time (h)
0
0.2
0.4
0.6
0.8
1
0
10
20
30
40


1.0
0.8
0.6
0.4
0.2
0.0
Proportion alive ($\bar{x}$ ± S.E.)
39
40
41
42
43
44
45
46
Temperature (°C)
E. warrae
En. formosa