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Use of life tables to quantify reproductive and developmental biology of *Gonatocerus triguttatus* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca vitripennis* (Hemiptera: Cicadellidae)

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Abstract

The reproductive and developmental biology of *Gonatocerus triguttatus* Girault, a parasitoid of the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), was determined at five constant temperatures in the laboratory; 15, 20, 25, 30, and 33 °C. At 25 °C, *G. triguttatus* maintained the highest successful parasitism rates with 25.1% of oviposition leading to emerging parasitoid larvae and lowest parasitism was observed at 15 °C with 7.3%. Lifetime fecundity was greatest at 25 °C and fell sharply as temperature either increased or decreased around 25 °C. Temperature had no effect on sex ratio of parasitoid offspring. Mean adult longevity was inversely related to temperature with a maximum of 20.6 days at 15 °C to a minimum of four days at 33 °C. Developmental rates increased non-linearly with increasing temperatures. Developmental rate data was fitted with the modified Logan model for oviposition to adult development times across each of the five experimental temperatures. Optimal, lower, and upper lethal, temperature thresholds for *G. triguttatus* were, 30.7, 10.4 and 38.8 °C, respectively. The lower developmental threshold estimated with linear regression was 10.57 °C, and is very close to the lower temperature threshold estimated by the modified Logan model. The linear regression of developmental rate across all five experimental temperatures indicated that 204 degree-days were required above the minimum threshold of 10.57 °C to complete development. Demographic parameters were calculated and pseudo-replicates for intrinsic rate of increase, net reproductive rates, generation time, population doubling time, and finite rate of increase were generated using the bootstrap method. Mean bootstrap estimates of demographic parameters were compared across temperatures using nonlinear regression.
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Keywords: Biological control; Bootstrap; Degree-days; Demographics; *Gonatocerus triguttatus*; *Homalodisca vitripennis*; *Homalodisca coagulata*; Intrinsic rate of increase; Life table; Net reproductive rate

1. Introduction

Gonatocerus triguttatus Girault (Hymenoptera: Mymaridae), deliberately imported from Texas USA and introduced into California USA in 2000 as part of a classical biological control program against the glassy-winged sharpshooter, *Homalodisca vitripennis* (Say) (Hemiptera: Cicadellidae) (Pilkington et al., 2005), is a solitary endoparasitoid that attacks eggs of sharpshooters in the cicadellid tribe Proconiini (Triapitsyn et al., 2002) and has a natural range that includes southeastern USA and northeastern Mexico where it is associated with *H. vitripennis*, (Triapitsyn and Phillips, 2000). Since establishing in southern California in the late 1980's, *H. vitripennis* has become a major economic pest (Pilkington et al., 2005) and is an efficient vector of the xylem-dwelling bacterial pathogen, *Xylella fastidiosa* (Pilkington and Hoddle, 2006a). One factor that may limit the successful establishment and impact of imported natural enemies used in a classical biological control program is imprecision in matching the environmental conditions in the natural enemy's home range with those in the area into which natural enemies are to be released (Goolsby et al., 2005; Hoddle, 2004).

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A thorough understanding and characterization of biological attributes of natural enemies such as degree-day requirements, and intrinsic rates of increase can have multiple practical applications, such as: (1) quantification of the reproductive and developmental biology of candidate natural enemies can assist with predicting potential establishment and population growth of natural enemies introduced into a new area (Godfray and Waage, 1991; Rochat and Gutierrez, 2001); (2) can aid preliminary evaluation of natural enemies for potential use in classical biological control; (3) assist with interpretation of natural enemy impact and spread in the field (Daane et al., 2005; Dahlsten et al., 2005), and (4) provide realistic values for parameters of models investigating incursion risks pertaining to movement of natural enemies into environments beyond those intended for permanent inhabitation.

Life tables are commonly used in studies addressing how the life expectancy of organisms may change if affected by environmental changes (Stäubli Dreyer et al., 1997; Tsai and Wang, 2001). Construction of life tables allows the calculation of key demographic characters such as intrinsic rate of increase, and net reproductive rate. Major shortfalls with life table construction from laboratory cohorts, namely that there is no replication as data from individuals in the study are collated for the production of one summary table, can be circumvented with intensive re-sampling procedures such as bootstrapping or jackknifing. This approach provides mean values and variance estimates for life table parameters of natural enemies which can be subjected to statistical tests (Pilkington and Hoddle, 2006a).

The bootstrap procedure involves randomly removing an individual from the life table and recalculating the statistical values of interest and is regarded as being more reliable for estimating variance in the life table values than jackknifing (Efron, 1981). The randomly removed individual is replaced prior to another being randomly selected and removed and the values once again recalculated. This approach essentially re-samples the experimental population (Meyer et al., 1986) and has been used regularly to generate mean life table parameters from unreplicated cohorts of natural enemies for statistical comparison across multiple temperatures (e.g., Efron, 1981; Meyer et al., 1986; Miller, 1974; Pilkington and Hoddle, 2006a).

Insects are poikliothermic, and their body temperatures are subject to change through heat exchange with the surrounding environment. Generally, as temperature increases, the development rate for poikilothermic organisms rises from a threshold of zero development to an optimal developmental rate before falling rapidly again to a developmental rate of zero, when the upper lethal threshold is reached. The modified Logan model (Lactin et al., 1995), describes this nonlinear relationship between developmental rate and temperature for insects, and estimates a developmental threshold above which development occurs, optimal temperature for development, and an upper lethal temperature at which death occurs. This study used two regression models in order to determine the lower, optimum and upper threshold temperatures and to estimate the required degree-days for development. The first, nonlinear, model was used to determine the lower, optimal and upper development thresholds for *G. triguttatus* from developmental rate data generated across five experimental temperatures in the laboratory. Linear regression, discarding data points that occurred at higher temperatures than the optimum temperature for development, was used to estimate degree-day accumulation necessary for *G. triguttatus* to complete development.

Improved understanding of the basic biology of *G. triguttatus*, a recently released and established natural enemy of *H. vitripennis* in California, will assist mass-rearing efforts of this parasitoid; optimize timing of inoculative field releases; facilitate better understanding of parasitoid spread and impact on *H. vitripennis* in various climatic zones in California; and will assist with targeted collecting for biotypes of *G. triguttatus* in the home range of *H. vitripennis* that may exhibit unique climatic adaptations that current parasitoid populations in California lack.

2. Materials and methods

2.1. Homalodisca vitripennis egg production

One hundred potted, insect-free 'Eureka' lemon trees, *Citrus limon* (L.) Burm., a cultivar preferred by *H. vitripennis* for egg laying (Irvin and Hoddle, 2004) were planted in one-liter pots, watered twice weekly with an initial application of fertilizer (Dynamite plant food; Enviro-Safe Laboratories, Inc., Miami, FL, USA) followed with a second application at six months. Trees were placed in two large (2.4 m × 1.8 m × 1.8 m), mesh screened walk-in cages located within a temperature-controlled greenhouse (6.5 m × 3.8 m × 3.8 m) maintained at 15–28 °C at Agricultural Operations Field Station, University of California, Riverside California. Daily field collections of *H. vitripennis* adults were sorted from other insects in the laboratory and approximately 500–1000 adults were added to these caged plants. Caged plants were inspected daily, and all *H. vitripennis* egg masses found deposited on leaves, were removed every 24 h and stored at 15 °C to ensure the age of eggs being presented to parasitoids was consistently within the range of 24–72 h of age, an age range readily utilized by *G. triguttatus* for parasitization (Irvin and Hoddle, 2005a).

2.2. Source of parasitoids and set up of experimental arenas

Gonatocerus triguttatus females used in studies were from the California Department of Food and Agriculture (CDFA) mass-rearing facility at Mt Rubidoux, Riverside California. *Homalodisca vitripennis* egg masses on 'Eureka' lemon leaves were placed in 130 ml plastic vial cages filled with deionized water (Pilkington and Hoddle, 2006a). A piece of parafilm "M" (Pechiney Plastic Packaging, Mena-

sha, WI, USA) was stretched and placed between the bottom vial and lid. Petioles were pushed through the parafilm in order to reduce incidence of parasitoid drowning and minimize condensation accumulation in the upper part of the cage.

2.3. Experimental temperatures and number of females used for experiments

Five individual growth cabinets (Percival Scientific Inc., Perry, IA) were set at 15 °C (±0.3 °C) (10 females set up), 20 °C (±0.6 °C) (13 females), 25 °C (±0.6 °C) (10 females), 30 °C (±0.5 °C) (10 females), and 33 °C (±0.3 °C) (15 females) with long days (14:10 L:D) and relative humidity (RH) set at 50%. Temperatures and RH in cabinets were measured every 180 min with HOBO data loggers (Onset Computer Co., Bourne, MA, USA).

2.4. Monitoring parasitoid progeny production

One-day-old mated female *G. triguttatus* were placed individually in cages containing approximately 30–40, 24- to 72-h-old *H. vitripennis* eggs and a 5% honey–water solution. After 24 h, females were moved, by aspiration, to a new cage containing fresh, unparasitized *H. vitripennis* eggs of the same age range. This procedure was repeated every 24 h until parasitoids died. The cause of death was recorded as natural or other (e.g., drowning in condensation or escape).

When parasitoid or *H. vitripennis* emergence was first detected from experimental egg masses, leaves were removed from cages, and placed in sealed, 9 mm Petri dishes (Becton Dickinson Labware, Franklin Lakes, NJ, USA) lined with moistened filter paper, maintained at the same experimental temperature, and checked daily for continued emergence. The length of time between oviposition and progeny emergence, sex of offspring, and percentage parasitism was recorded for every egg mass at each experimental temperature (15 °C, $n = 71$; 20 °C, $n = 148$; 25 °C, $n = 212$; 30 °C, $n = 109$; 33 °C, $n = 54$). At temperatures where instances of no emergence of either parasitoid or host was observed (i.e., 33 °C), *H. vitripennis* eggs were dissected and the number of developed but dead parasitoid larvae and pupae were recorded and used as estimates of parasitism. At each experimental temperature, 60 *H. vitripennis* eggs were placed in separate cages not containing parasitoids as controls. Preoviposition, oviposition to adult development times, and oviposition rates were calculated using all female parasitoids regardless of their cause of death. Total progeny, mean daily progeny, and sex ratio were calculated using data from emerged, viable parasitoids that died of natural causes.

2.5. Calculation of demographic growth parameters

Time from oviposition to emergence, adult parasitoid survivorship rates, daily fecundity, and sex ratio of offspring at each experimental temperature were used to construct $l_\chi m_\chi$ life tables from which demographic growth parameters were calculated. Only data from adult parasitoids that died naturally were used for calculation of demographic growth parameters (15 °C, $n = 10$ mated females; 20 °C, $n = 10$; 25 °C, $n = 10$; 30 °C, $n = 9$; 33 °C, $n = 10$). The following demographic parameters were calculated:

1. Net reproductive rates, $R_o = \sum l_\chi m_\chi$, (Deevey, 1947).
2. Mean generation time, $T_c = \sum \chi l_\chi m_\chi / R_o$ (Deevey, 1947). Direct estimates of generation time were calculated from individual parasitoid offspring development time from oviposition to adult emergence. These calculations concurred with estimated generation times.
3. The intrinsic rate of natural increase, r_m, (Birch, 1948). The value of r_m is iterated until the equation $1 = \sum l_\chi m_\chi \exp(-r_m \chi)$ is solved.
4. Finite rate of increase, $\lambda = \exp(r_m)$ (Birch, 1948).
5. Population doubling time, $T_d = \ln 2 / r_m$, (Carey, 1989).

Mean demographic parameter estimates with standard errors were generated using bootstrap pseudo-replication of $l_\chi m_\chi$ life table data. Female parasitoids dying prematurely from other causes were discarded for these analyses (Pilkington and Hoddle, 2006a).

The new dataset calculated by bootstrapping contains many pseudo-replicates and no adjustment for the removed individuals is necessary, and bias in the generated mean R_o value ($R_{o.adj}$) is reduced with the equation:

$$R_{o.adj} = 2 \times R_{o.all} - R_{o.bootstrapped} \text{(Meyer etal., 1986)}.$$

From this bootstrap analysis, mean and variance estimates for each demographic parameter of interest (i.e., equations 1–5 above) were calculated for *G. triguttatus* at each experimental temperature.

2.6. Developmental rates, temperature thresholds, and degree-day calculations

Developmental rates for each experimental temperature were calculated as the reciprocal time in days from oviposition to the emergence of adult parasitoids. These calculations were based on means from clutches. The modified Logan model was fitted to the reciprocal of mean developmental time in days for each temperature (Lactin et al., 1995). The non-linear fitted line from the modified Logan model intercepted the x-axis and identified the lower developmental threshold. The optimum temperature for insect development was identified as the peak in the fitted line and the upper lethal threshold was identified as the point where the line crossed the x-axis at a higher temperature. The highest temperature, 33 °C, was omitted from the fitting of the linear regression model to the same data in order to obtain a more accurate indication of the linear portion of the data. Degree-day requirements were calculated using the inverse slope of this fitted linear regression line (Campbell et al., 1974) and the lower developmental threshold

estimated by the modified Logan model was verified using the linear interception point.

2.7. Statistical analysis

Pre-oviposition times, mean adult longevity, successful oviposition rates (oviposition resulting in viable offspring), parasitism rates (oviposition events that include dissected eggs containing *G. triguttatus* larvae that did not emerge), and lifetime fecundity, and mean bootstrapped demographic parameters (Pilkington and Hoddle, 2006a) were compared with ANOVA and Tukey's Studentized Range Test at the 0.05 level of significance. Direct estimates of generation times, and daily fecundity were compared using Kruskal–Wallis non-parametric tests and means separated using a median test at the 0.05 level of significance (SPSS Inc., 1999).

The demographic parameter means were subjected to non-linear regression (SAS Institute, 2002) in order to estimate the affect of different temperatures on life table values outside the experimental temperature range (Lactin et al., 1995). The pseudo-values for R_o, r_m, T_c, T_d, and λ were analyzed with ANOVA and Tukey's Studentized Range Test ($P = 0.05$) to determine if there were statistical differences between the temperatures and quadratic regression lines fitted to the data (SAS Institute, 2002). All statistical tests and model fitting were performed using SAS 9.1 (SAS Institute, 2002).

3. Results

3.1. Partial life tables and developmental and reproductive estimates

Life tables were constructed for the number of *G. triguttatus* adults entering each age class and their realized and actual mortality rates (Table 1). Analysis of variance showed that mean adult longevity, the length of time from adult emergence to natural death, was significantly different between temperatures ($F = 19.576$, df = 4, 44, $P < 0.001$) and was greatest with a value of 20.6 days at 15 °C, declining to a low of 4.1 days at 33 °C (Table 2).

Oviposition that led to emergence of offspring was highest at 25 °C (Table 2) and was significantly different between temperatures ($F = 18.014$, df = 4, 596, $P < 0.001$). At 25 °C, 25.15% of *H. vitripennis* eggs presented to parasitoids produced viable progeny. Parasitism rates decreased to 7.34 and 20.07% at 15 and 33 °C, respectively (Table 2). Survivorship curves for *G. triguttatus* are shown in Fig. 1.

Preoviposition was longest at 15 °C ($F = 7.900$, df = 4, $P < 0.001$), total progeny ($F = 39.744$, df = 4, 45, $P < 0.001$) and mean daily offspring ($\chi^2 = 258.233$, df = 4, $P < 0.001$) was highest at 25 and 33 °C, respectively (Table 2). Direct estimates of development time (i.e., mean number of days [±SE] from oviposition to emergence of adult parasitoids) derived from temperature development studies were longest at 15 °C (Table 2). There were no statistically significant differences in progeny sex ratio across experimental temperatures (Table 2).

3.2. Demographic growth parameters

Mean net reproductive rate (R_o) ($F = 758500$, df = 4, 49995, $P < 0.001$; $y = -0.5959x^2 + 29.2x - 302.31$, $R^2 = 0.8366$, Fig. 2a), intrinsic rate of increase (r_m) ($F = 7447000$, df = 4, 49995, $P < 0.001$; $y = -0.0015x^2 + 0.0822x - 0.8828$, $R^2 = 0.9245$, Fig. 2b) and finite rate of increase (λ) ($F = 6934000$, df = 4, 49995, $P < 0.001$; $y = -0.0017x^2 + 0.0966x - 0.0453$, $R^2 = 0.9065$) were all significantly different between temperatures and were highest for *G. triguttatus* reared at a constant 25 °C. Population doubling times, T_d, were lowest when parasitoids were reared at 25 and 30 °C ($F = 1802000$, df = 4, 49995, $P < 0.001$; $y = 0.1148x^2 - 6.3267x + 87.907$, $R^2 = 0.9656$, Fig. 2c). Mean generation time, T_c, was lowest at 33 °C ($F = 1823000$, df = 4, 49995, $P < 0.001$; $y = 0.1802x^2 - 10.832x + 173.99$, $R^2 = 0.987$, Fig. 2d).

Table 1
Partial life table for adult *Gonatocerus triguttatus* reared at five constant temperatures and age class in days is representative of the adult parasitoid life stage only

Age class	l_x [a]					d_x [b]					q_x [c]					M_r [d]				
Age class	15°	20°	25°	30°	33°	15°	20°	25°	30°	33°	15°	20°	25°	30°	33°	15°	20°	25°	30°	33°
0–3	10	8	9	9	14	0	1	0	0	8	0.00	0.13	0.00	0.00	0.57	0.00	0.13	0.00	0.00	0.57
4–7	10	7	9	9	6	0	0	0	3	5	0.00	0.00	0.00	0.33	0.83	0.00	0.00	0.00	0.33	0.36
8–11	10	7	9	6	1	3	3	1	4	1	0.30	0.43	0.11	0.67	1.00	0.30	0.38	0.11	0.44	0.07
12–15	7	4	8	2	0	1	0	5	2	0	0.14	0.00	0.63	1.00		0.10	0.00	0.56	0.22	
16–19	6	4	3	0	0	1	3	3	0	0	0.17	0.75	1.00			0.10	0.38	0.33		
20–23	5	1	0	0	0	1	1	0	0	0	0.20	1.00				0.10	0.13			
24–27	4	0	0	0	0	1	0	0	0	0	0.25					0.10				
28–31	3	0	0	0	0	3	0	0	0	0	1.00					0.30				

[a] l_x, Number entering stage.
[b] d_x, Number dying in stage.
[c] q_x, Apparent mortality, the proportion dying within the age class.
[d] M_r, Real mortality, the proportion dying within the age class reflected as a function of the number entering the first age class.

Table 2
Mean adult longevity (±SE), mean preoviposition period (±SE), mean daily fecundity, lifetime fecundity (±SE), direct generation time (±SE), female sex ratio of progeny (±SE) and successful parasitism rate (±SE) of mated female *Gonatocerus triguttatus* at each experimental temperature

	Temperature (°C)				
	15	20	25	30	33
Adult longevity (days)	20.60 ± 2.75a	15.57 ± 1.87ab	15.33 ± 0.78ab	10.00 ± 0.73bc	4.07 ± 0.76c
Preoviposition period (days)	2.78 ± 1.05a	0.25 ± 0.13b	0.00 ± 0.00c	0.11 ± 0.11bc	0.00 ± 0.00bc
Total progeny	22.70 ± 4.48a	46.78 ± 4.39b	87.11 ± 4.91c	53.67 ± 4.14b	21.31 ± 3.59a
Mean daily progeny	1.25 ± 0.22a	3.68 ± 0.41b	6.19 ± 0.56c	5.75 ± 0.52cd	6.43 ± 1.32d
Mean developmental time (days)	46.52 ± 0.76a	22.34 ± 0.22b	12.99 ± 0.12c	10.77 ± 0.24d	10.96 ± 0.17d
Sex ratio (% female offspring)	64.13 ± 3.74a	60.71 ± 2.53a	68.93 ± 2.03a	67.14 ± 2.34a	72.61 ± 4.23a
Parasitism rate (%)	7.34 ± 1.20a	16.62 ± 1.63b	25.15 ± 1.91c	21.32 ± 1.77bc	20.07 ± 3.89bc

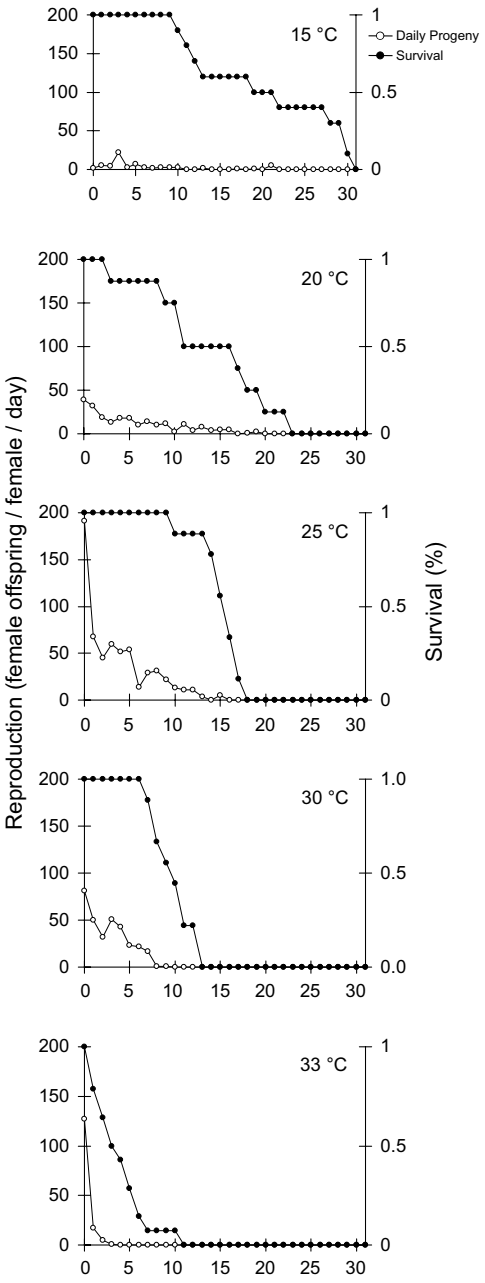

Fig. 1. Mean (±SE) observed age-specific female progeny from individual parasitoids and survivorship data for *Gonatocerus triguttatus* at five temperatures.

3.3. Developmental rates, temperature thresholds, and degree-days

The development rate for *G. triguttatus* was slowest at 15 °C, increasing until 30 °C after which higher temperatures failed to have a statistically significant effect ($F = 2067.411$, df = 4, 590, $P < 0.0001$). The developmental rate was nonlinear and the fitted Modified Logan model was highly significant ($F = 1754.36$, df = 4, 590, $P < 0.0001$) (Fig. 3). The fitted model converged on a lower developmental threshold for *G. triguttatus* of 10.43 °C. The modified Logan model estimated upper maximum temperature for development at 38.82 and 30.74 °C was the estimated as the optimal temperature for development. Linear regression indicated immature *G. triguttatus* required a total of 204.08 degree-days to complete development from oviposition to adult emergence and the lower temperature threshold for development was estimated at 10.57 °C from this analysis, which is similar to that estimated by the modified Logan model (10.43 °C).

4. Discussion

Gonatocerus triguttatus has been mass released in southern California since 2002, and, although small localized populations appear to have established, the widespread establishment of this species has failed to become robust and abundant (D. Morgan [CDFA] pers. comm. 2006). The failure of this species to establish in the central grape growing areas of California has been an ongoing concern and there is little evidence to suggest that acclimatization or adaptation is likely to allow a wider establishment of this species. Two potential reasons may exist for these localized low density populations of *G. triguttatus*: (1) not enough time has elapsed since release and establishment for *G. triguttatus* to have reached its full potential. (2) In the field, this parasitoid is an ineffective competitor with the self-introduced and omnipresent *G. ashmeadi*. Laboratory studies suggest interspecific competition with *G. ashmeadi* may be severely limiting to *G. triguttatus* (Irvin and Hoddle, 2005b; Irvin et al., 2006). In comparison to *G. ashmeadi*, *G. triguttatus* has reduced longevity, parasitizes fewer *H. vitripennis* eggs, spends more time resting and grooming, and in some instances devotes little time to

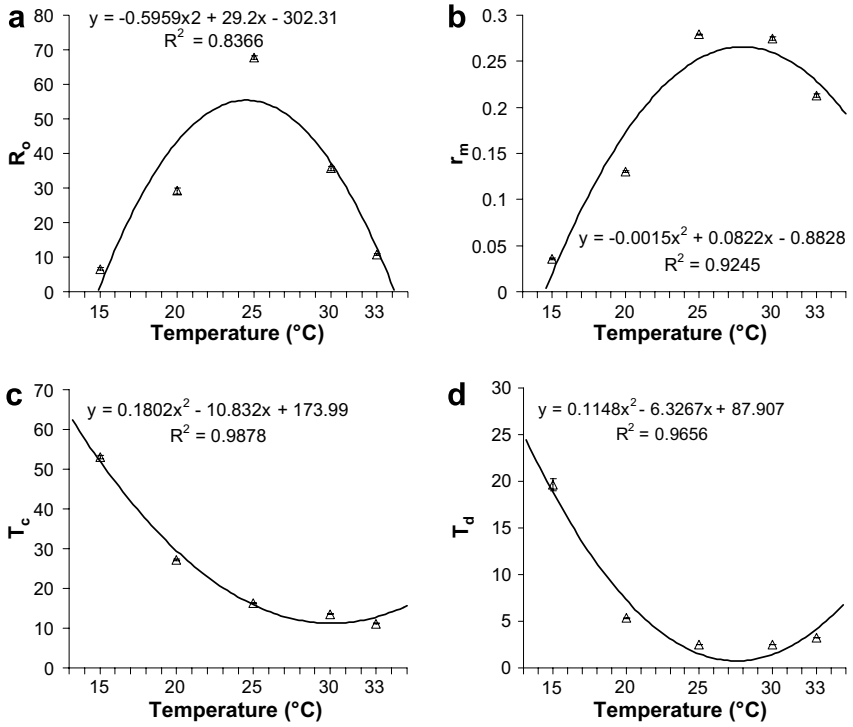

Fig. 2. Fitted quadratic lines for life table statistics R_o (a), r_m (b), T_d (c) and T_c (d) for *Gonatocerus triguttatus* at each of five experimental temperatures.

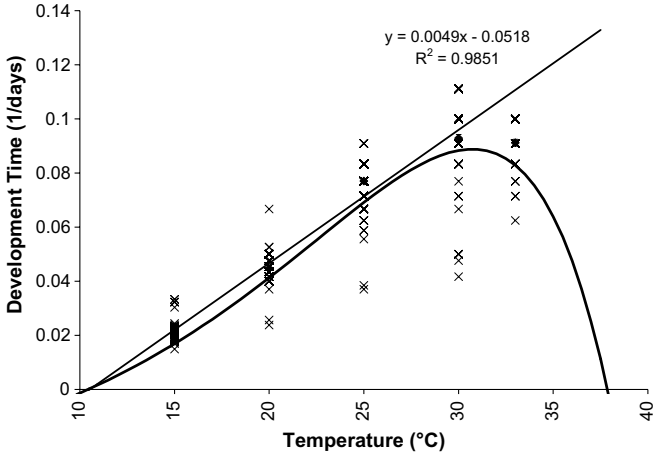

Fig. 3. The developmental rate of *Gonatocerus triguttatus* from time of oviposition to adult emergence expressed as the relationship of developmental rates and temperature fitted to the modified Logan model as described by Lactin et al. (1995) and using linear regression (Campbell et al., 1974). Values presented are means for each female's offspring rather than individual values.

defending host patches from competitors (Irvin and Hoddle, 2005b; Irvin et al., 2006). The reduced impact of *G. triguttatus* as a regulating factor of populations of *H. vitripennis* in southern California may also be influenced by climatic conditions in the invaded areas. Low temperatures over winter appear to reduce or prevent oviposition by *H. vitripennis* for extended periods which results in a shortage of hosts for *G. triguttatus* and other mymarid parasitoids attacking *H. vitripennis* (Pilkington et al., 2005). Further, *G. triguttatus* has not been recorded from an alternative host in California, *H. liturata*, whereas the common *G. ashmeadi* is often associated with this common native sharpshooter. These factors, interspecific competition, cool temperature intolerance, and possible non-exploitation of native cicadellid hosts during periods of target scarcity, may prevent *G. triguttatus* manifesting robust populations in climatically-favorable areas of California.

The survival rates and longevity for adult *G. triguttatus* were highest at 15 °C although progeny production was negligible at this temperature. The number of offspring produced by individual parasitoids was greatest at 20–30 °C with each female producing two to three times more offspring than females maintained at 15 or 33 °C. The net reproductive rate, R_o, was highest at 25 °C, being 80.3–84.0% higher than the highest (33 °C) and lowest (15 °C) temperatures evaluated, respectively. Population doubling time, T_d, was lowest at 25 and 30 °C, reflecting lower numbers and survivorship rates of offspring produced. Population doubling times were 7.8 and 1.3 times greater at 15 and 33 °C, respectively, indicating that much longer periods of time are needed at these temperatures for populations to complete development, and to increase in number.

Laboratory results presented here indicate that modest changes in constant temperature can affect the reproductive capabilities of *G. triguttatus* and, possibly, the parasitoid's ability to adversely impact populations of its host, *H. vitripennis*. The development of offspring has been predicted to occur at temperatures above a developmental threshold around 10.43–10.57 °C (lower estimate from linear regression; higher estimate from modified Logan model) and

below the upper lethal temperature of 38.8 °C. Daily weather data for ten years over the period 1995–2004 recorded at the University of California, Riverside Agricultural Operations Facility, a major citrus production center where *H. vitripennis* research is conducted, indicated that over the year, daily mean minimum and maximum temperatures were 3.8 °C (±1.31 SE) and 37.33 °C (±1.09 SE), respectively, which appear to be within the upper tolerance level for *G. triguttatus* as indicated from the results of the modified Logan model analysis conducted in this study and within the lower tolerance levels as this parasitoid has been collected numerous times from this citrus orchard since its release at this site in 2002 (Hoddle unpublished).

Temperature can have a significant impact on R_o estimates for *G. triguttatus*. The fitted quadratic model for R_o, a measure of a population's growth rate, indicated that at approximately 14.9 °C the value of R_o falls below 1.0, indicating that parasitoid population growth will cease and begin to contract. During this 10 year span, the weather station at the University of California, Riverside Agricultural Operations Facility recorded the average daily temperature falling below 14.9 °C 127 times or 35% of the year. The ten-year average daily temperature in Riverside falls below 14.9 °C in a single, discrete block of 100 days typically over the period November to March. During this three month time span, temperatures fluctuate from a minimum of 3.8 °C to a maximum high temperature of 22.89 °C. Although temperatures rise above the development threshold required by *G. triguttatus*, calculations indicate that the population would accumulate enough degree-days to complete 2.5 generations in this time. Temperatures may rise enough to prompt sporadic oviposition by parasitoids if host eggs are available but persistent low temperatures over winter will retard parasitoid population growth. Host availability notwithstanding, this suggests populations of *G. triguttatus* in Riverside California would contract markedly over the period November–March each year because of impaired reproductive performance at temperatures below 14.9 °C periods for prolonged periods. Consequently, demographic data from studies completed here, coupled with long-term weather data sets for southern California, may explain why populations of *G. triguttatus* are not more common, widespread or have been particularly successful in attacking abundant *H. vitripennis* egg masses in California.

As a caveat for this work, we emphasize that all data presented here were produced by providing single parasitoid females unlimited host resources and by removing all adverse influences that could affect reproduction (e.g., interspecific and intraspecific competition for egg masses, predation, and fluctuating temperatures). Thus extrapolation of laboratory data derived at constant temperatures to definitively explain field observations or valid predictions of spread and impact by *G. triguttatus* needs to be assessed and considered with caution (Baker, 2002). The value in this work is as a comparison between two geographic regions for the same species or, as is the case with *G. ashmeadi*, as a comparison against another organism where identical studies have been undertaken (Pilkington and Hoddle, 2006a,b).

By understanding the effects temperature and climate have on the development and reproduction of potential biological control agents and optimizing the match to receiving environments, a greater degree of successful natural enemy establishment and efficacy may be achieved (Goolsby et al., 2005). It has been proposed that environmental conditions such as temperature, rainfall, and humidity should be monitored in a proposed biological control agent's native region in order to identify conditions that may prevent their successful establishment in introduced areas (Goolsby et al., 2005). Life table and developmental statistics, such as those presented here, provide valuable tools for the evaluation of potential biological control agents for release in proposed areas that are climatically different to the native area. This biologically-based assessment has demonstrated ecological utility and determination of the effect of climatic factors on parasitoid performance may greatly enhance the selection of efficacious natural enemies for use in classical biological control programs (Goolsby et al., 2005; Pilkington and Hoddle, 2006a,b).

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