REPRODUCTIVE AND DEVELOPMENTAL BIOLOGY OF *GONATOCERUS ASHMEADI*, AN EGG PARASITOID OF THE GLASSY-WINGED SHARPSHOOTER

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ABSTRACT
The reproductive and developmental biology of *Gonatocerus ashmeadi* Girault, a parasitoid of the glassy-winged sharpshooter *Homalodisca coagulata* (Say), was determined at five constant temperatures in the laboratory; 15; 20; 25; 30; and 33°C. At 30°C, *G. ashmeadi* maintained the highest successful parasitism rates with 46.1% of parasitoid larvae surviving to adulthood. Lifetime fecundity was greatest at 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 days at 15°C to a minimum of eight days at 33°C. Developmental rates increased nonlinearly with increasing temperatures. Developmental rate data was fitted with the modified Logan model for oviposition to adult development times to determine lower developmental threshold (1.1°C, and 7.16°C estimated by linear regression), optimal developmental temperature (30.5°C), and upper lethal temperature threshold (37.6°C). Linear regression of developmental rate for temperatures 15-30°C indicated that 222 degree-days were required above a minimum threshold of 7.16°C to complete development. Demographic parameters were calculated and pseudoreplicates for intrinsic rate of increase (r_m), net reproductive rates (R_o), generation time (T_c), population doubling time (T_d), and finite rate of increase (λ) were generated using the bootstrap method. Mean bootstrap estimates of demographic parameters were compared across temperatures using ANOVA and nonlinear regression.

INTRODUCTION
The mymarid parasitoid species *Gonatocerus ashmeadi* Girault, *G. triguttatus* Girault, *G. morrilli* Howard, and *G. fasciatus* Girault are the most common natural enemies associated with the insect pest *Homalodisca coagulata*, the glassy-winged sharpshooter (GWSS), in it's home range of southeastern USA and northeastern Mexico (Triapitsyn and Phillips, 2000). The parasitoid *G. ashmeadi* is a self-introduced resident of California and most likely came into the state in parasitized *Homalodisca coagulata* eggs (Vickerman *et al.*, 2004) and has established widely in association with *H. coagulata*.

One factor that can limit the success of the establishment of natural enemies is mismatching the environmental conditions favored by the introduced agent with those that predominate in the receiving range (Hoddle, 2004). Quantification of the reproductive and developmental biology of a natural enemy is paramount to predicting, planning, and promoting the establishment and population growth of introduced agents. This can be enhanced by determining demographic characteristics such as day-degree requirements for immature development, population doubling times and lifetime fecundity for estimating population growth rates at various temperatures and for comparison with the target pest and other species of biological control agents. Determining the introduced control agent's reproductive and developmental biology and environmental requirements with that of the host will allow for a greater understanding of factors affecting biological control of GWSS.

The following work was undertaken to provide information on the reproductive and developmental biology of the solitary endoparasitoid of GWSS eggs, *G. ashmeadi*. These data will provide knowledge of the natural enemy's life cycle in relation to utilization of GWSS eggs at different temperatures, and may improve the understanding of optimal timings of releases for biological control purposes, as well as improve the efficiency of mass rearing of these insects. In addition to improving release and rearing strategies, this information will target foreign exploration for strains of *G. ashmeadi* for possible introduction into California and also identify geographical areas that will be conducive to the use of this species as biological control agent following GWSS establishment in various parts of California and in areas such as Tahiti and Hawaii where GWSS has recently invaded, and perhaps elsewhere in the South Pacific if GWSS continues to invade additional tropical islands.

OBJECTIVES
1. Examine the developmental and reproductive biology of *G. ashmeadi* at five different temperatures in order to determine its day-degree requirements, and demographic statistics, and to better understand this parasitoid's developmental and reproductive biology.

RESULTS
Life tables were constructed for the number of *G. ashmeadi* entering each age class and their realized and actual mortality rates. Analysis of variance showed that mean adult longevity, the length of time from adult emergence to natural death, was significantly different between temperatures (F=6.155, df=4, 44, P<0.001) and longevity was greatest with a value of 20.0 days at 15°C, declining to a low of 7.9 days at 33°C (Table 1).

Mean net reproductive rate (R_o) (F=73857.9, df=4, 4995, P<0.001), intrinsic rate of increase (r_m) (F=732354, df=4, 4995, P<0.001) and finite rate of increase (λ) (F=683820, df=4, 4995, P<0.001) were all significantly higher for *G. ashmeadi* reared at a constant 25°C, 30°C and 30°C, respectively (Table 2). Population doubling times, T_d, showed a statistically significant difference (F=178515, df=4, 4995, P<0.001) and were lowest when parasitoids were reared at 30°C. Mean generation time, T_c, was significantly lower at 33°C (F=1821157, df=4, 4995, P<0.001) (Table 2). Quadratic lines were fitted to the means for each life table parameter and accounted for 79.6% to 99.7% of the observed variance (Figure 1).

The developmental rate for *G. ashmeadi* was nonlinear and the fitted Modified Logan model was highly significant (F=1292.27, df=4, 495, P<0.005) (Figure 2). The fitted model converged on a lower developmental threshold for *G. ashmeadi* of 1.1°C. The upper maximum lethal temperature for development was estimated at 37.6°C, and 30.5°C was the estimated as the optimal temperature for development. Linear regression indicated immature *G. ashmeadi* required a total of 222 degree-days to complete development of from oviposition to adult emergence and the lower temperature threshold for development was estimated at 7.16°C from this linear regression analysis.

Table 1. Mean adult longevity (±SE), mean preoviposition period (± SE), mean daily fecundity, lifetime fecundity (± SE) and female sex ratio of progeny of mated female *Gonatocerus ashmeadi* at each experimental temperature.

	Temperature (°C)				
	15	20	25	30	33
Adult longevity (days)	20.00±2.69a	15.90±2.02ab	12.00±1.23bc	10.56±1.36bc	7.90±0.98c
Preoviposition period (days)	4.53±0.486a	0.61±0.293b	0.182±0.125b	0.227±0.113b	0.235±0.106b
Total progeny	7.07±1.767a	46.35±8.387b	63.75±8.362b	59.88±6.931b	10.37±1.562a
Mean daily progeny	0.24±0.098a	1.66±0.353ab	2.24±0.685b	2.10±0.685b	0.37±0.152a
Sex ratio (% female offspring)	65.11±7.348a	65.03±6.807a	71.54±6.020a	64.54±5.690a	65.08±6.461a

Table 2. Mean demographic statistics (± standard error) generated from $l_\chi m_\chi$ life tables that were bootstrapped to produce pseudo-values for *G. ashmeadi*. R_o = net reproductive rate; T_c = generation time; r_m = intrinsic rate of increase; λ = finite rate of increase; T_d = doubling time in days. Values with different letters indicate significant differences at 0.05 level of confidence.

Temp °C	R_o	T_c	r_m	λ	T_d
15	8.30±0.291a	44.49±0.097a	0.05±0.001a	1.02±0.001a	14.51±0.249a
20	35.70±0.856b	25.77±0.161b	0.15±0.001b	1.16±0.001b	4.62±0.033b
25	55.94±1.023c	16.61±0.029c	0.26±0.001c	1.30±0.001c	2.66±0.011c
30	45.33±1.014d	12.61±0.103d	0.33±0.001d	1.39±0.002d	2.11±0.009d
33	9.20±0.142e	12.37±0.038e	0.18±0.001e	1.20±0.002e	3.80±0.029e

CONCLUSIONS

Gonatocerus ashmeadi is the key mymarid parasitoid species contributing to the biological suppression *H. coagulata* in its native area of southeastern U.S.A. and northeastern Mexico (Triapitsyn and Phillips, 2000). The impact of *G. ashmeadi* as a regulating factor of populations of *H. coagulata* in California is, in contrast to efficacy in the home range, substantially lower (Pilkington et al., In Press).

Temperature can have a significant impact on R_o estimates for *G. ashmeadi*. The fitted quadratic model for R_o, a measure of a population's growth rate, indicated that at approximately 14.6°C the value of R_o falls below 1.0, indicating that parasitoid population increase will cease and begin to contract. Host availability notwithstanding, this suggests populations of *G. ashmeadi* in Riverside California would contract markedly over the period November-March each year because of impaired reproductive performance at temperatures below 14.6°C periods for prolonged periods.

The success of a biological control agent is measured by the mortality it inflicts on its target which is in part a function of its reproductive and developmental activity across a range of temperatures (Nahrung and Murphy, 2002). The results from this study suggest that *G. ashmeadi* operates most effectively at moderate to high temperatures. Identifying the optimal temperature for reproduction and development of *G. ashmeadi*, will greatly aid mass-rearing efforts, using day-degree models to predict geographic range, to assess generational turnover in various locales in comparison to GWSS and to optimize releases of natural enemies into a field environment.

There is a need for this type of work on population demographics, developmental and reproductive biology to be reproduced for *G. triguttatus* and particularly *H. coagulata*. Efforts towards meeting these two shortcomings are either underway or will be commenced very soon. There is a large gap in the knowledge regarding the biology of the pest and its temperature requirements and identifying and understanding the areas of overlap, or lack thereof, between the pest and biological control agents. A greater degree of precision in the prediction of the efficacy of biological control agents in areas yet to be invaded by *H. coagulata* would be possible with improved understanding of the performance of GWSS at various temperatures.

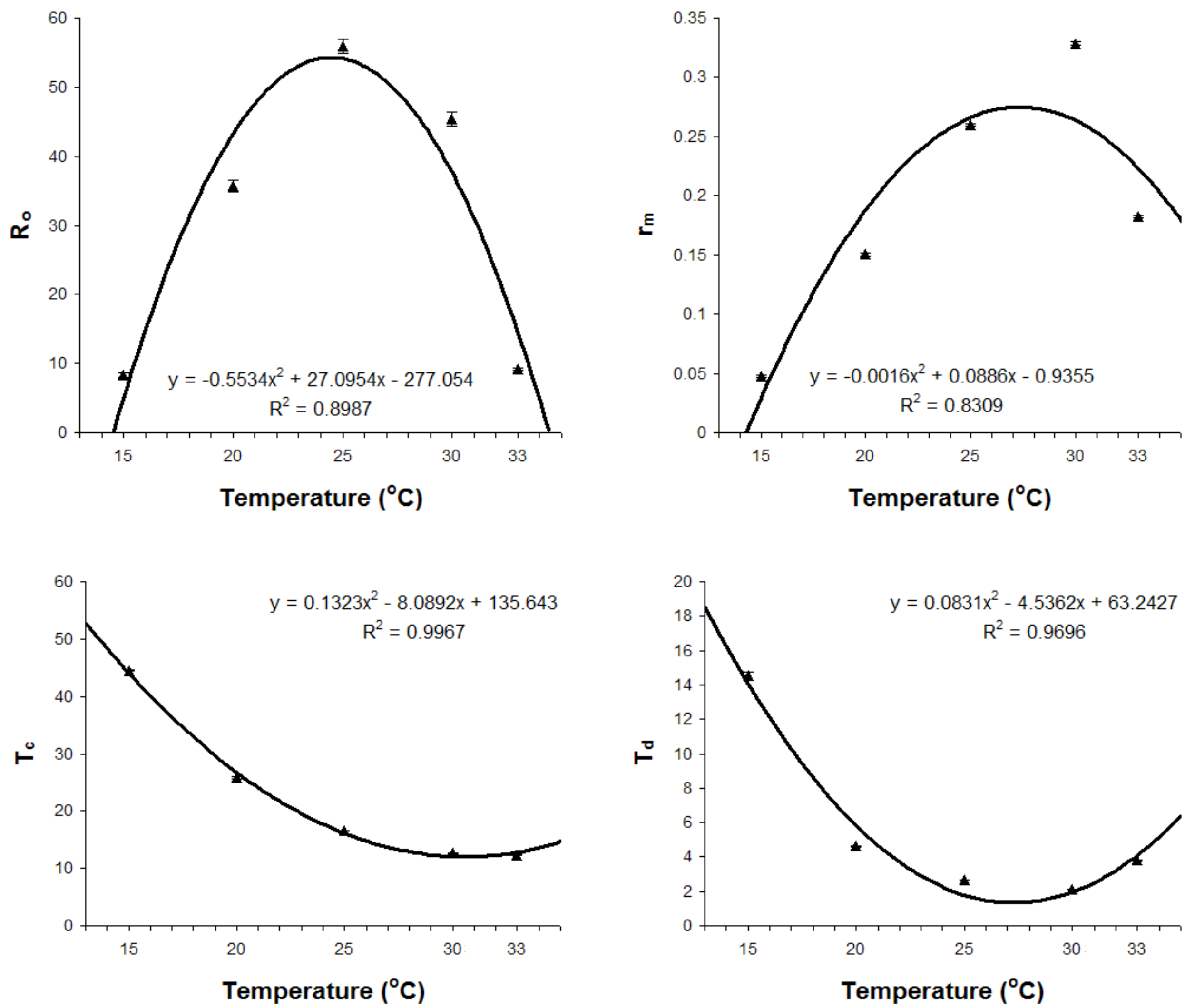

Figure 1. Fitted quadratic lines for life table statistics R_o, r_m, T_c and T_d for *Gonatocerus ashmeadi* at each experimental temperature.

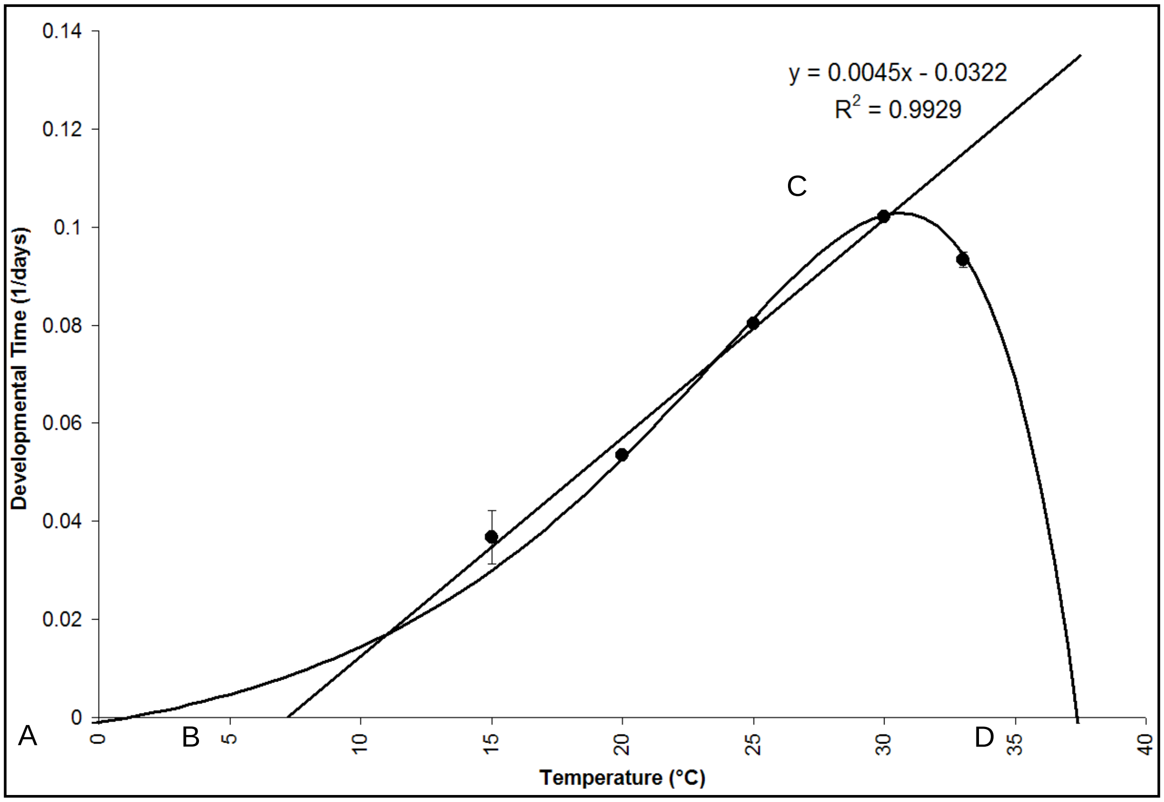

Figure 2. The developmental rate of *Gonatocerus ashmeadi* from time of oviposition to adult emergence expressed as the relationship of developmental rates and temperature fitted to the modified Logan model as described by Lactin et al. (1995) and using linear regression (Campbell et al., 1974). Lower developmental threshold (calculated with modified Logan model [A = 1.1^{o}C] and linear regression [B = 7.16^{o}C]), optimal development (C = 30.5^{o}C) and upper lethal threshold (D = 37.6^{o}C) are indicated.

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