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Maximum realised lifetime parasitism and occurrence of time limitation in Gonatocerus ashmeadi (Hymenoptera: Mymaridae) foraging in citrus orchards

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RESEARCH ARTICLE

Maximum realised lifetime parasitism and occurrence of time limitation in *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae) foraging in citrus orchards

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The relationship between body size (hind tibia length), <12 h egg load, wing wear and parasitoid age was used to estimate realised lifetime parasitism of recently dead *Gonatocerus ashmeadi* collected in a citrus orchard. Under prevailing field conditions and methodology assumptions, it was estimated that female *G. ashmeadi* lived on average for 183 ± 17 degree-days, parasitised a total of 87 ± 9 *Homalodisca vitripennis* eggs, and died with 34 ± 5 eggs remaining in the ovaries. Only 17% of dead *G. ashmeadi* died with no mature eggs suggesting that 83% of *G. ashmeadi* were not egg limited at time of death. Estimates of realised lifetime parasitism for female *G. ashmeadi* under prevailing field conditions in July and August in a southern California citrus orchard indicated that time of year had a significant effect on reproductive output. Additionally, live *G. ashmeadi* captured daily during June through August 2006 had body size, egg load and wing wear recorded to detect possible monthly changes in parasitoid age and egg load. Foraging *G. ashmeadi* captured alive in June were older and oviposited more eggs in the field compared with August. Only 0.5% of live *G. ashmeadi* were captured with no mature eggs in their ovaries indicating that the vast majority of live *G. ashmeadi* were not egg limited.

Keywords: egg load; realised lifetime parasitism; time limitation; wing wear

1. Introduction

Gonatocerus ashmeadi Girault (Hymenoptera: Mymaridae) is a small solitary egg parasitoid [1.28–1.76 mm in length (Triapitsyn, 2006)], and is the key natural enemy attacking egg masses of the glassy-winged sharpshooter, *Homalodisca vitripennis* [Germar; Hemiptera: Cicadellidae; formally *H. coagulata* (Takiya, McKamey, & Cavichioli, 2006)], in California (USA). *H. vitripennis* is xylophagous and is an economically significant vector of the xylem-limited bacterium, *Xylella fastidiosa*, which causes disease in a variety of important plants including Pierce's disease in grapes, almond leaf scorch, alfalfa dwarf, phony peach disease and oleander leaf scorch (Blua, Phillips, & Redak, 1999; UCOP, 2000; Varela, Smith, & Phillips, 2001). Pierce's disease threatens grape production which is valued at $3.86 billion

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and economic activity associated with the grape industry, especially wine production in California, is estimated to be in excess of $61.5 billion (CDFA, 2012).

Substantial laboratory work has been conducted to parameterise basic aspects of *G. ashmeadi* reproduction (Irvin & Hoddle 2005a, 2005b, 2006, 2007; Irvin, Hoddle, & Castle, 2007), development (Chen, Leopod, & Boetel, 2008; Pilkington & Hoddle, 2006) and behaviour (Chen, Leopold, & Harris, 2006; Krugner, Johnson, Daane, & Morse, 2008). Additionally, Irvin and Hoddle (2009) investigated ovigeny, egg maturation and egg resorption in *G. ashmeadi* under laboratory conditions and reported that *G. ashmeadi* is synovigenic. Although basic aspects of the biology of *G. ashmeadi* are well understood in the laboratory, field-level assessments of parasitism of *H. vitripennis* eggs by individual *G. ashmeadi* have not been quantified.

Jepsen, Rosenheim, and Matthews (2007) used a previously obtained relationship between initial egg load at time of birth and body size, measured using tibia length, to estimate field reproductive success of *Anagrus erythroneurae* Trjapitzin & Chiappini (Hymenoptera: Mymaridae), a parasitoid of the grape leafhopper, *Erythroneura elegantula* Osborn (Hemiptera: Cicadellidae). This simple method for estimating realised fecundity in the field was possible because *A. erythroneurae* is pro-ovigenic and adult females emerge with their full lifetime complement of mature eggs (Jervis, Heimpel, Ferns, Harvey, & Kidd, 2001). Consequently, depletion of this stock can be measured and used to infer the number of hosts attacked in the field up to the time of death (Jepsen et al., 2007). Field estimates of realised fecundity for synovigenic parasitoids, species that continue to mature eggs throughout their reproductive life, are more complicated to measure (Jervis et al., 2001). Due to the difficulty of determining oviposition rates among synovigenic parasitoids, some studies have estimated daily fecundity of parasitoids foraging in the field rather than lifetime fecundity (Lee & Heimpel, 2008). Despite the difficulties associated with obtaining measures under field conditions, Heimpel, Rosenheim, and Mangel (1998) estimated lifetime fecundity of a synovigenic parasitoid, *Aphytis aonidiae* (Mercet; Hymenoptera: Aphelinidae), in the field using previously attained laboratory and field estimations of parasitoid mortality, and the relationships between host size and parasitoid egg load at emergence, encounter rate, handling times and egg maturation rate.

The contribution of individual *G. ashmeadi* females to the natural biological control of *H. vitripennis* in the field is unknown, therefore, we sought to estimate realised lifetime parasitism at time of death for *G. ashmeadi* in a citrus orchard [a highly preferred host for *H. vitripennis* (CDFA, 2012)] that was not treated with pesticides using previously attained laboratory data on the relationships of female size and egg load, egg maturation and wing wear and parasitoid age (Irvin & Hoddle, 2009). These data were used to estimate the lifetime reproductive success of female *G. ashmeadi* that had recently died of natural causes and were captured in traps as they fell from citrus trees. The results presented here are an attempt to estimate the maximum possible impact individual female *G. ashmeadi* could have on *H. vitripennis* in a pesticide-free citrus orchard. Additionally, to detect temporal changes in parasitoid age, egg load and biological control potential throughout the summer, a second group of female *G. ashmeadi* were captured alive in the field and their age and reproductive success at time of capture were estimated. We sought to determine whether individuals from the two different groups of *G. ashmeadi*, captured dead or

captured live, had been limited by the time available to locate and parasitise hosts (time limitation) or by the number of eggs available for oviposition (egg limitation; Rosenheim, 1996; Sevenster, Ellers, & Driessen, 1998). Finally, to aid interpretation of potential differences in age and reproductive success of field-collected *G. ashmeadi* across months, the numbers of adult *H. vitripennis*, *G. ashmeadi* and *H. vitripennis* eggs were monitored in the same citrus orchard.

2. Materials and methods

2.1. *Estimating realised lifetime parasitism of individual* G. ashmeadi *collected dead in the field*

Funnel traps were used to capture recently dead female *G. ashmeadi* falling from untreated citrus trees at University of California, Riverside, CA, Agricultural Operations Facility (UCR Ag. Ops.). Funnel traps were deployed five days a week from 18 July 2006 to 1 September 2006. Funnel traps consisted of a 473-ml plastic cup (Smart and Final Chef's Review, 16 oz Food Containers, Amerifoods Trading Co., Los Angeles, CA) placed inside a white polystyrene container (28 × 22.5 × 18 cm, wall thickness 4 cm; ThermoSafe Insulated EPS Container Outside Dimensions, Hayward, CA) spray-painted black (Rust-oleum Paint for Plastics, Rust-oleum, Vernon Hills, IL). Black traps were used to reduce the likelihood of funnel traps attracting live parasitoids (Lobdell, Yong, & Hoffmann, 2005; Romeis, Shanower, & Zebit, 1998).

Dry ice was packed around the plastic cup polystyrene reservoir that would hold recently dead *G. ashmeadi* that fell from trees into the funnel trap. A 2.2-cm hole was cut in the lid of the plastic cup and polystyrene container. A red plastic funnel (20 cm diameter, 1.89 l Blitz Funnel, Custom Accessories Inc., Niles, IL), spray-painted black, was positioned through the holes in the polystyrene container and plastic cup so that dead insects falling from trees were funnelled in the plastic cup surrounded in dry ice and immediately preserved. On each sampling date, 40 funnel traps were placed underneath the canopies of 40 randomly selected orange trees from approximately 9 am until 5 pm. At the end of each day, traps were collected and returned to the laboratory where *G. ashmeadi* were removed with fine forceps by the antennae (to prevent wing damage).

Female *G. ashmeadi* were dissected, the numbers of mature, immature and partially reabsorbed eggs at time of death were counted, hind tibia length (HTL) was measured, forewings were slide mounted and the number of broken setae on wings was counted following protocols outlined in Irvin and Hoddle (2009). 'Partially reabsorbed eggs' were defined as mature eggs that had partially disintegrated, possibly during the process of resorption (see Irvin & Hoddle, 2009). Total egg load was calculated as the total number of mature, immature eggs and partially reabsorbed eggs.

HTL was used to estimate the number of eggs at emergence for each female using the relationship [y = (252.77 × HTL) – 77.38] between initial egg load (<12 h egg load) and HTL, as previously determined in Irvin and Hoddle (2009). The previously attained relationship between female age and wing wear in the laboratory, y = (7.77 × number of broken hairs per female) + 62.61, was used to estimate the age of each female at time of death (Irvin & Hoddle, 2009). Female age was used to estimate the number of eggs matured since female emergence using the relationship y = (0.33 ×

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female age) – 9.58, as previously described in Irvin and Hoddle (2009). Collectively, data on egg load at death and these two relationships were used to estimate the mean number of *H. vitripennis* eggs parasitised by each female *G. ashmeadi* prior to death and collection in funnel traps by using the following equation:

$$\text{Eggs at emergence} + \text{Eggs matured} - \text{Total egg load} = \text{Number of eggs oviposited}$$

This equation is partially based on laboratory-derived data, and makes the following assumptions about conditions in the field: (1) dead *G. ashmeadi* collected in the field had not initiated egg resorption. It is known that resorption is initiated after 163 degree-days (or five days at 26°C) without hosts (Irvin & Hoddle, 2009). Field surveys indicate that *H. vitripennis* eggs were very abundant in citrus orchards during July and August when dead *G. ashmeadi* females were being collected in funnel traps (Hoddle, 2010), and it was highly unlikely that individual *G. ashmeadi* would not encounter hosts for oviposition during the 163 degree-day period needed to initiate resorption; (2) a food supply for *G. ashmeadi* was available in the field. In fact, softscale (*Coccus hesperidum* L.) was present and sometimes locally abundant in the citrus orchard where funnel traps were deployed. Honeydew from this pest is an excellent food for *G. ashmeadi* (Irvin et al., 2007); (3) environmental conditions (e.g., temperatures, predation) in the field were not significantly deleterious for *G. ashmeadi* survival and forging. Environmental parameters were evaluated in this study; and (4) there was no premature mortality of *G. ashmeadi* in the field, (e.g., from predation, starvation or excessive heat). Our goal was to determine maximum realised fecundity of *G. ashmeadi*. These assumptions are examined later in Section 4.

Mean estimated egg load, estimated age, estimated realised lifetime parasitism and an estimated ovigenic index [i.e., the number of mature eggs at female emergence divided by potential lifetime fecundity (Jervis et al., 2001)] were calculated for the sampling period in July and August 2006. These parameter estimates were statistically compared between months using *t*-tests on untransformed data at the 0.05 level of significance (SAS Institute, 1990). Finally, to estimate the contribution of individual *G. ashmeadi* to biological control of *H. vitripennis* in the field, the overall mean estimated age, estimated realised lifetime parasitism and estimated ovigenic index were calculated.

2.2. *Temporal changes in age, egg load and biocontrol potential of field-foraging* G. ashmeadi

In southern California, *G. ashmeadi* exhibit two distinct generations per year in approximately May/June and August (Hoddle, 2010; Pilkington et al., 2005). To detect these temporal changes in parasitoid age, egg load and biological control potential, *G. ashmeadi* were captured daily by sweep netting from citrus located at UCR Ag. Ops. from 6 June 2006 to 30 August 2006. Collections were made from 6.30 am to 9.00 am, five days per week, on citrus trees within 500 m of the funnel trap study site. Sweep net captures were emptied into field cages (34 × 32 × 38 cm) and returned to the laboratory. *G. ashmeadi* were aspirated into 130-ml plastic vials, labelled with collection date and frozen. A subsample of 1–6 female *G. ashmeadi* for each sampling date was dissected, and egg load, HTL and wing wear were measured and age and the number of eggs oviposited in the field were calculated as described

above. Census data were separated into three one-month intervals. The effect of month on the total number of eggs in ovaries at time of capture (raw data), estimated egg load at time of birth as estimated from HTL (Box Cox 3 transformed prior to analysis), parasitoid age as estimated from wing wear (log transformed) and the number of eggs laid in the field until time of capture (square root transformed) was determined using one-way analysis of variance (ANOVA) in SAS Institute (1990). The mean, standard error of the mean (SEM) and range were calculated for each month and parameter of interest.

2.3. H. vitripennis *and* G. ashmeadi *population studies and climate statistics*

To aid interpretation of potential differences in age, egg load and realised parasitism of field-collected *G. ashmeadi* females across months, the numbers of adult *H. vitripennis*, *G. ashmeadi* and *H. vitripennis* eggs were monitored in the field. Ten non-pesticide-treated 'Eureka' lemon trees were randomly selected from 20 rows of mixed citrus trees located at UCR Ag. Ops. These trees were within 500 m of the site where funnel traps were deployed and of similar age and management conditions. Every two weeks from June to August 2006, two one-minute searches for *H. vitripennis* adults were conducted on the north and south sides of each tree on foliage that was located between 1 m and 2 m from the ground. Additionally, a five-minute search for unemerged *H. vitripennis* egg masses was conducted around each tree within this 1–2 m band. Unemerged egg masses were removed and the number of eggs within each mass was counted in the laboratory using a binocular microscope. Stems of leaves with egg masses were placed into individual vials filled with tap water and left for three weeks to allow parasitoids to emerge. The number of male and female *G. ashmeadi* that emerged from egg masses was recorded for each tree by sampling date. Sampling dates were separated into three one-month intervals. The effect of sampling month on the number of adult *H. vitripennis* counted during field searches, *H. vitripennis* eggs and male and female *G. ashmeadi* emerging from egg masses was determined using Wald tests, and contrast tests at the 0.05 level of significance were used to separate means using SAS Institute (1990).

Daily average air temperature, maximum daily air temperature, relative humidity and precipitation at UCR Ag. Ops. were downloaded from the CIMIS weather database (i.e., Station 44; http://www.cimis.water.ca.gov/cimis/dataInfoType.jsp). The number of adult *H. vitripennis* recorded for each sampling method, the number of *G. ashmeadi* and weather statistics were calculated for June, July and August 2006 and compared between months using a longitudinal log-linear analyses in SAS Institute (1990). Contrast tests at the 0.05 level of significance were used to separate effects of months. Precipitation occurred only in August, therefore, Fisher's exact test at the 0.5 level of significance was used to compare this mean with zero (McDonald, 2008).

2.4. *Determining the relationship between mean egg load of living* G. ashmeadi *and* '*explanatory variables*'

Data for each sample of 1–6 female *G. ashmeadi* that were collected alive (the same data as in Section 2.2) were averaged for each sampling date. The relationships between: (1) total egg load at capture (raw data) and explanatory variables and (2) number of mature eggs at capture (square root transformation) and explanatory

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variables were determined using multivariate regression analysis (Mendenhall & Sincich, 2003). Normality assumptions were satisfied. The 'explanatory variables' used in analyses were month, average temperature on day of capture, maximum temperature on day of capture, mean temperature during the last five days before capture, host egg density, *H. vitripennis* density, female *G. ashmeadi* density, HTL and wing wear of *G. ashmeadi*. A Pearson's correlation coefficient matrix (Mendenhall & Sincich, 2003) was used to determine correlations between explanatory variables. Average temperature on day of capture, maximum temperature on day of capture and *H. vitripennis* density were removed from multivariate regression analyses because they were highly correlated with other variables (i.e., to avoid multicollinearity; see Section 3). For the multivariate regression analysis, squared and cubed terms were included for host egg density and female *G. ashmeadi* density to normalise distributions. After conducting the full multivariate regression model, non-significant terms were removed from the model and this final model was refitted. Multivariate regression was also used to obtain estimates of the coefficients in the final model. All analyses were performed in SAS Institute (1990).

3. Results

3.1. *Estimating realised lifetime parasitism of individual* G. ashmeadi *collected dead in the field*

A total of 18 dead female *G. ashmeadi* were collected in funnel traps and used for the analyses. There were no significant differences in HTL and estimated egg load at the time of female emergence (initial egg load) for dead *G. ashmeadi* collected in funnel traps deployed in July and August 2006 (Figure 1). Estimated age and estimated realised lifetime parasitism of parasitoids collected in funnel traps in July were significantly greater (100 degree-days and 51 eggs higher, respectively) compared with dead females collected in August (Figure 1). The overall mean (±SEM) realised lifetime parasitism and mean (±SEM) ovigeny index were 87 ± 9 eggs and 0.93 ± 0.10, respectively. The average age of dead female *G. ashmeadi* collected in funnel traps was 183 ± 17 degree-days [approximately eight days at 26°C (Irvin & Hoddle, 2009)]. Total egg load ranged from 2 to 65, and only three females (17% of total females collected in funnel traps) died with zero eggs (including mature, non-mature and partially reabsorbed eggs) in their ovaries (Figure 2a). Similarly, 17% of *G. ashmeadi* contained no mature eggs indicating that 83% of females were not egg limited at time of death (Figure 2a). Females had on average 34 ± 5 eggs remaining in their ovaries at time of death in the field. One partially resorbed egg was counted in the ovaries of two (11%) dead field-collected *G. ashmeadi*, while no other partially reabsorbed eggs were found.

3.2. *Temporal changes in age, egg load and biocontrol potential of field-foraging* G. ashmeadi

A total of 220 live female *G. ashmeadi* were captured from sweep net sampling and used for the analyses. Live *G. ashmeadi* captured in the field in June were on average 31.2 degree-days older and had oviposited on average 15 more eggs than females captured in August (Figure 3). Estimated initial egg load of *G. ashmeadi* captured in August was four eggs higher than those captured in July. Total egg load did not

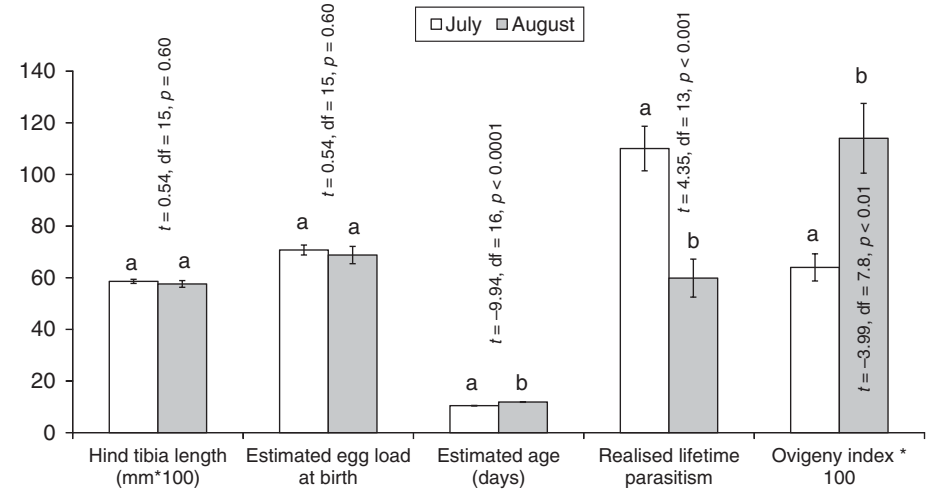

Figure 1. Egg load data, realised *lifetime* fecundity and estimated age of dead *G. ashmeadi* captured in funnel traps located in citrus orchards in July and August 2006 (different letters indicate significant differences between months; error bars indicate ±SEM).

differ significantly between months. Foraging *G. ashmeadi* had total egg loads ranging from 4 to 88 (Figure 2b). Only one female (0.5%) contained no mature eggs indicating that the vast majority (99.5%) of foraging *G. ashmeadi* were not egg limited at time of capture (Figure 2b). Between 1 and 6 partially reabsorbed eggs were counted in the ovaries of 21% of live *G. ashmeadi*, while the ovaries of one female (0.5%) contained 18 partially reabsorbed eggs.

3.3. H. vitripennis *and* G. ashmeadi *population studies and temperature relationships*

Populations of adult *H. vitripennis* were up to 37-fold higher in July (28 adults per tree) compared with June and August, and the number of individual *H. vitripennis* eggs was up to 17-fold higher in August (16.7 eggs per tree; Figure 4). The number of *G. ashmeadi* emerging from *H. vitripennis* egg masses increased by 2.4 males and 2.3 females *G. ashmeadi* per citrus tree, respectively, from June to August 2006 (Figure 4).

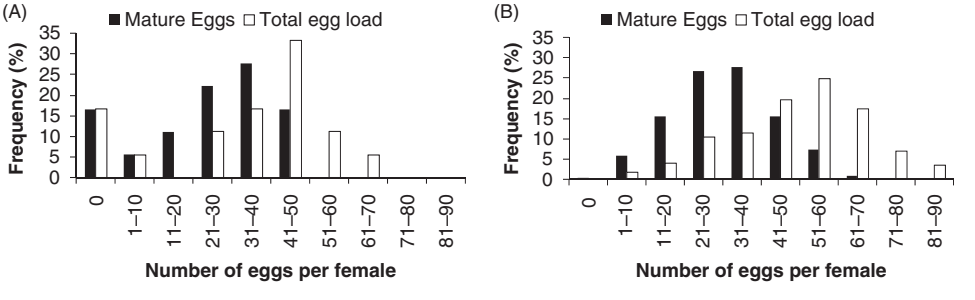

Figure 2. The frequency of distribution of egg loads counted in ovaries of (A) dead *G. ashmeadi* captured in funnel traps during July and August 2006 and (B) living *G. ashmeadi* captured in sweep net samples during June, July and August 2006.

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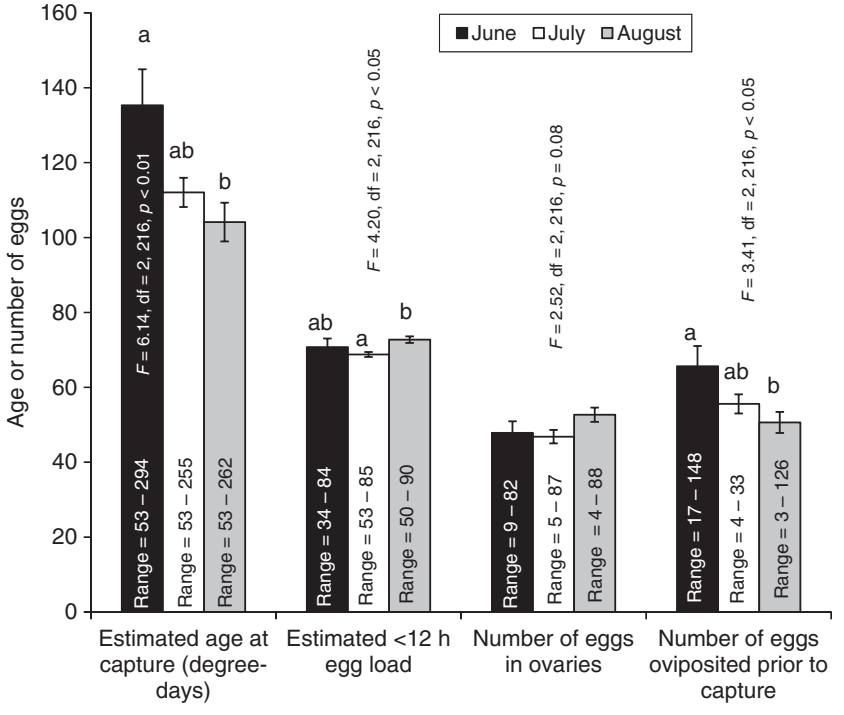

Figure 3. Egg load data, estimated age and the number of eggs female *G. ashmeadi* oviposited prior to capture in sweep net sampling conducted in June, July and August 2006 (different letters indicate significant differences between months; error bars indicate ±SEM).

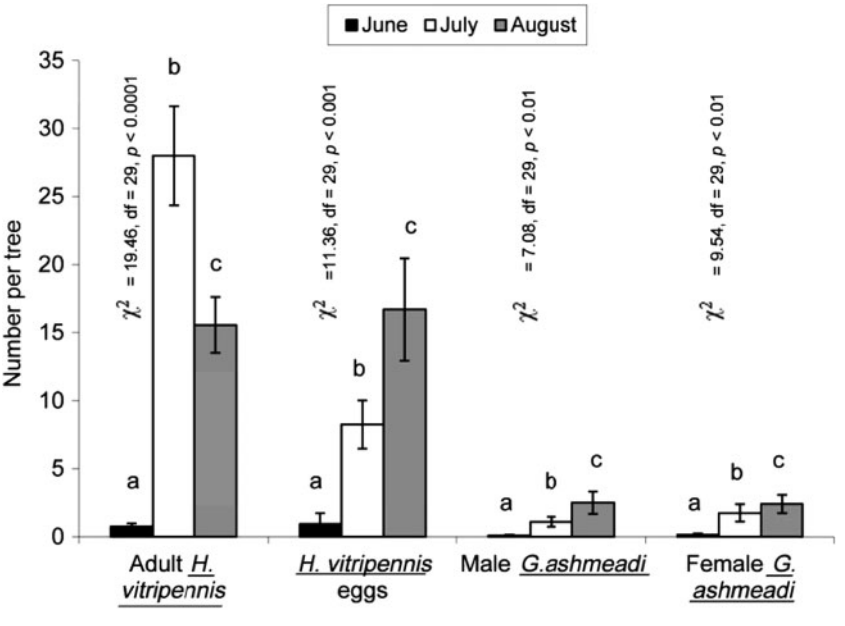

Figure 4. The mean (±SEM) number of adult *H. vitripennis*, *H. vitripennis* eggs and male and female *G. ashmeadi* emerging from egg masses collected during 2-minute visual searches in Eureka lemon trees at UCR Ag. Ops., in June, July and August 2006.

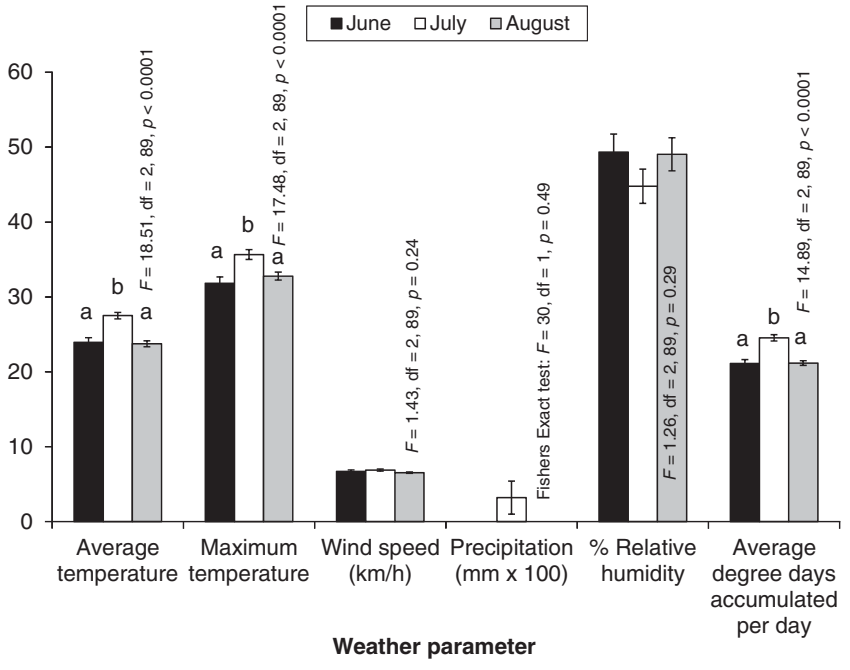

Figure 5. Weather data for University of California Riverside (Station 44) downloaded from CIMIS *website* for June, July and August 2006 (different letters indicate significant differences between months for each weather parameter; error bars indicate ±SEM).

Average daily temperature, maximum daily temperature and degree-days accumulated per day were respectively up to 3.8°C, 3.8°C and 3.4 degree-days higher in July compared with June and August (Figure 5). There were no significant differences in wind speed, precipitation and percentage relative humidity between months (Figure 5). On 11 days during the field study (13% of the total number of days), the maximum temperature temporarily exceeded 36.7°C, the upper threshold for development for *G. ashmeadi* (Pilkington & Hoddle, 2006). Maximum daily temperature reached 43.8°C in August and exceeded 33°C on 51 days during the field study (59% of the total number of days over which this study was conducted).

3.4. Determining the relationship between egg load and explanatory variables

The Pearson's correlation matrix indicated that temperature on day of capture was strongly correlated with average temperature for the previous five days before capture (Pearson's correlation coefficient = 0.70, $p < 0.0001$) and maximum temperature on day of capture (Pearson's correlation coefficient = 0.90, $p < 0.0001$). Adult *H. vitripennis* density was strongly correlated with female *G. ashmeadi* density (Pearson's correlation coefficient = 0.71, $p < 0.0001$). Therefore, to avoid multicollinearity, average temperature on day of capture, maximum temperature and adult *H. vitripennis* density were removed from multiple regression analyses. For mature eggs, the full multiple regression model indicated that HTL ($F = 0.05$, df = 1, $p = 0.82$) and wing wear ($F = 0.66$, df = 1, $p = 0.42$) of *G. ashmeadi* had no significant effect on the number of mature eggs and these variables were removed

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Table 1. Statistical results (df = 2 for 'month' and 1 for remaining variables) and estimates of coefficients for the final multivariate regression model conducted to determine the relationship between significant explanatory variables and the number of mature eggs counted in ovaries of living *G. ashmeadi* captured in the field (R^2 = 0.46).

	Test statistics		Estimates of coefficients	
Explanatory variable	*F*-Value	*p*-Value	Estimate	Standard error
Mean temperature of previous five days before capture	7.59	0.006	−0.07	0.03
Host egg density	9.35	0.003	0.78	0.25
Host egg density[2]	6.13	0.01	−0.04	0.01
Host egg density[3]	4.08	0.05	0.0004	0.0002
G. ashmeadi density	31.45	<0.0001	−8.35	1.49
G. ashmeadi density[2]	43.06	<0.0001	4.13	0.63
G. ashmeadi density[3]	48.53	<0.0001	−0.65	0.09
Month	3.31	0.04		
June			−0.23	0.37
July			0.42	0.24
August			0	.
Intercept			7.86	0.69

[2]term squared
[3]term cubed

from the regression model. Analyses of the remaining variables showed significant effects on the number of mature eggs in live *G. ashmeadi* (Table 1). There was a positive correlation between number of mature eggs and host egg density (Table 1). There was a negative correlation between number of mature eggs and two variables: mean temperature of the previous five days before capture and female *G. ashmeadi* density (Table 1). The number of mature eggs was expressed by the following equation derived from the multiple regression model:

$$\text{Mature eggs} = 7.86 - 0.07\,t + 0.78\,h - 0.04\,h^2 + 0.0004\,h^3 - 8.35\,F + 4.13\,F^2 - 0.65\,F^3 - 0.23\,Jn + 0.42\,Jy,$$

where t = mean temperature of previous five days before capture, h = host egg density (mean number of eggs counted in 2 minutes), F = female *G. ashmeadi* density, Jn = June and Jy = July.

For total egg load, the multivariate regression model was not significant (F = 1.02, df = 2, p = 0.36) for month, and *G. ashmeadi* wing wear had no significant effect (F = 3.70, df = 1, p = 0.06) on mean egg load of captured living *G. ashmeadi*. All remaining variables had significant effects on total egg load (Table 2). There was a positive correlation between total egg load and two variables: host egg density and HTL (Table 2). There was a negative correlation between total egg load and two variables: mean temperature of the previous five days before capture and female *G. ashmeadi* density (Table 2). Total egg load was expressed by the following equation derived from the multivariate regression model:

$$\text{Total egg load} = 63.29 - 1.07\,t + 12.30\,h - 0.61\,h^2 + 0.01\,h^3 - 117.94\,F + 54.50\,F^2 - 7.95\,F^3 + 38.93\,\text{HTL}$$

(where t = mean temperature of previous five days before capture, h = host egg

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Table 2. Statistical results (df = 1) and estimates of coefficients for the final multivariate regression model used to determine the relationship between significant explanatory variables and total egg load of living *G. ashmeadi* captured in the field (R^2 = 0.41).

	Test statistics		Estimates of coefficients	
Explanatory variable	*F*-Value	*p*-Value	Estimate	Standard error
Mean temperature of previous five days before capture	10.45	0.001	−1.07	11.31
Host egg density	18.88	<.0001	12.27	0.33
Host egg density[2]	14.96	0.0001	−0.61	2.82
Host egg density[3]	12.50	0.0005	0.01	0.16
G. ashmeadi density	31.54	<.0001	−177.94	0.002
G. ashmeadi density[2]	36.06	<.0001	54.50	21.00
G. ashmeadi density[3]	37.53	<.0001	−7.95	9.08
HTL	5.07	0.03	38.93	1.30
Intercept			63.30	17.30

[2]term squared
[3]term cubed

density (mean number of eggs counted in 2 minutes), *F* = female *G. ashmeadi* density and HTL = hind tibia length).

4. Discussion

4.1. *Estimating realised lifetime parasitism of individual* G. ashmeadi *collected dead in the field*

Higher estimated realised parasitism of dead female *G. ashmeadi* collected in funnel traps observed in July was not attributable to a higher abundance of hosts or differences in female size. Furthermore, the number of female *G. ashmeadi* emerging from *H. vitripennis* egg masses collected in July and August was equivalent, indicating that potential competition for host eggs between individual *G. ashmeadi* did not affect realised parasitism. Temperature can have a significant effect on egg load of female parasitoids (Rosenheim & Rosen, 1991). The average daily temperature recorded in July and August was 27.5°C and 23.7°C, respectively. Pilkington and Hoddle (2006) demonstrated that the optimal temperature for *G. ashmeadi* oviposition and lifetime fecundity is 25°C; therefore, warmer temperatures in July were less favourable for *G. ashmeadi* oviposition. Wing wear as an indicator of age may have led to an overestimation of relative age of *G. ashmeadi* collected in July since the higher temperatures which occurred in this month may have increased the foraging activity of parasitoids. This may have caused *G. ashmeadi* to find more hosts while simultaneously increasing wing wear (Allsopp, 1985) which would have correlated with a higher estimated age and realised parasitism. The highly variable breakage rates of wing setae between caged and field insects (Lee, Leibee, & Heimpel, 2006) make it difficult to apply this relationship to estimate absolute age of field-captured insects. However, wing wear indices may be useful in estimating and comparing relative age between groups of insects within the same environment (Lee & Heimpel, 2008). Despite these uncertainties, this study concludes that time of year had a significant effect on relative age and reproductive output for female *G. ashmeadi*.

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We sought to investigate the maximum possible impact an individual female *G. ashmeadi* is likely to have on the target pest *H. vitripennis* over the course of an individual's lifetime. Under prevailing field conditions and methodology assumptions, *G. ashmeadi* females that died of natural causes in the field realised just 72% of their optimal 256 degree-days lifespan (Pilkington & Hoddle, 2006) or 78% of the average 14-day lifespan under optimal laboratory conditions providing a suitable food source (Irvin & Hoddle, 2007). Furthermore, field-collected parasitoids realised only 60% of their potential lifetime parasitism (Irvin & Hoddle, 2009). The actual impact of *G. ashmeadi* on *H. vitripennis* in the field is likely lower than estimated here because the estimation of realised parasitism is based on optimal laboratory conditions which are likely not to occur in the field (see below), and *G. ashmeadi* may parasitise eggs of another host, *Homalodisca liturata* Ball in addition to *H. vitripennis.* Al-Wahaibi and Morse (2010) showed that in the summer months approximately 90% of *Homalodisca* spp. egg masses at Ag. Ops were *H. vitripennis*, while the remaining egg masses were *H. liturata.*

Female *G. ashmeadi* contained, on average, 34 mature eggs in their ovaries at time of death, and the majority (83%) of females were time limited and not egg limited. These results confirm that dead *G. ashmeadi* did not reach their maximum reproductive potential in the field. Time-limited parasitoids risk dying with eggs in their ovaries which reduces the potential lifetime efficacy of natural enemies (Rosenheim, 1996).

There is some evidence that floral resources can lead to increases in parasitism rates in agricultural environments (Lavandero, Wratten, Shishehbor, & Worner, 2005; Scheid, Thies, & Tscharntke, 2011; Tylianakis, Didham, & Wratten, 2004), although this is not always the case (Heimpel & Jervis, 2005). Given the synovigenic nature of *G. ashmeadi* under optimal laboratory conditions (Irvin & Hoddle, 2009) and the absence of host feeding by this species, non-host food sources are necessary for individual females to produce more eggs than with which they emerged. When provided supplemental food, females survived up to 405% longer and produced up to 378% more progeny in the laboratory compared to unfed controls (Irvin & Hoddle, 2007). The citrus orchard used in this study was completely devoid of a vegetative understorey that could have provided nutrition to parasitoids via nectar in flowers. However, softscale (and other honeydew-producing hemipterans) was present in the citrus orchard where funnel traps were deployed and softscale honeydew is an excellent food for increasing *G. ashmeadi* survival rates in the laboratory (Irvin et al., 2007). It is unknown whether *G. ashmeadi* is able to access softscale honeydew in the field, especially if ants are tending this pest. Parasitoids lived an estimated 8 days in the field, whereas, female *G. ashmeadi* only live for 2.5 days without food in the laboratory (Irvin & Hoddle, 2007). Therefore, it is likely parasitoids were feeding on some type of resource in the field. This leads us to suggest that provision of plant resources in the field (e.g., planting an appropriate flowering understorey) could improve biological control of *H. vitripennis* by *G. ashmeadi* in promoting synovigeny, longevity and fecundity.

Although the current study aimed to estimate the maximum lifetime parasitism under optimal field conditions, actual realised lifetime parasitism of *G. ashmeadi* in the field may be substantially lower than that estimated here because a number of parameters were estimated from data derived from controlled laboratory studies. Realised lifetime fecundity of parasitoids in the laboratory and field may differ due

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to the differences in mortality (Koenig & Albano, 1987; Weisser, Volkl, & Hassell, 1997), temperature (Rosenheim & Rosen, 1991), egg resorption, host encounter rates and wing wear. Premature adult mortality in this study could have occurred from predation (e.g., spiders or ants), starvation (see above) and environmental extremes (e.g., high summer temperatures). *G. ashmeadi* have an upper developmental temperature threshold of 37.6°C (Pilkington & Hoddle, 2006). The maximum daily temperature exceeded this upper threshold on 11 days (i.e., 13% of the total number of days this study was conducted) before dropping below 37.6°C as temperatures cooled in the evening. It is unknown what effect these temporary temperature highs may have had on adult *G. ashmeadi* morality rates. Mortality of adult parasitoids from predation can prematurely reduce longevity and realised lifetime fecundity (Heimpel, Rosenheim, & Mangel, 1997a). Predation rates of *G. ashmeadi* foraging for *H. vitripennis* eggs or food sources in citrus are unknown and parasitoids that died prematurely from predation were not collected in funnel traps. However, predation has been recorded for similarly small-sized parasitoids (e.g., *Aphytis* spp.; Heimpel et al., 1997a).

Egg maturation and oviposition rates are influenced by temperature (Rosenheim & Rosen, 1991). The estimates of lifetime parasitism used here were based on oviposition and egg maturation rates of female *G. ashmeadi* under a constant laboratory temperature of 26°C. Although the average daily temperature (24–27°C) during the field study was comparable to the optimal temperature for *G. ashmeadi* oviposition and lifetime fecundity (25°C; Pilkington & Hoddle, 2006), maximum daily temperatures exceeded 33°C on 51 days during this study (i.e., 59% of the total number of days). Pilkington and Hoddle (2006) demonstrated that lifetime fecundity was reduced by 84% when temperature was increased from a constant 25°C to a constant 33°C in temperature-controlled cabinets. Therefore, there may have been periods during the day where oviposition ceased and egg maturation rates were reduced because of heat stress.

Egg resorption was not included in the calculation of lifetime parasitism because host eggs were prevalent in the field during the course of the study (Hoddle, 2010). However, results showed that two dead *G. ashmeadi* collected in funnel traps contained one partially reabsorbed egg (i.e., a mature egg that had degraded), indicating that some females had autolysed mature eggs, possibly enabling them to redirect energy to promote foraging, survival or development of newer mature eggs (Collier, 1995; Irvin & Hoddle, 2009; Rivero-Lynch & Godfray, 1997). Similarly, egg resorption has been ignored in other studies for estimating field parasitism rates (Casas et al., 2000; Heimpel et al., 1998).

Access to carbohydrates and host encounter rates can affect parasitoid lifetime fecundity (Heimpel, Rosenheim, & Kattari, 1997b; Irvin & Hoddle, 2007). A food resource in the citrus orchard where this study was conducted may not have been found by 11% of field-captured *G. ashmeadi* that died of natural causes and exhibited egg resorption despite *H. vitripennis* eggs being plentiful. It is likely that host encounter rates may be lower in the field because full-grown citrus trees have high structural complexity which may slow host location (Hoddle, 2003). In comparison, parasitoids readily find hosts in small simple experimental arenas used in laboratory studies from which estimates of fecundity and attack rates are typically based (Irvin, Hoddle, & Suarez-Espinoza, 2009; Pilkington & Hoddle, 2006).

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Finally, the number of additional eggs produced by *G. ashmeadi* since emergence in the field was based on the absolute age of females as estimated from wing wear experiments that were conducted in the laboratory. Higher temperatures in the field in comparison to the laboratory may have caused females to fly more and thus break setae at higher rates. If this occurred, then this study may have over-estimated the number of additional eggs matured since emergence and realised lifetime parasitism. Alternatively, lifetime parasitism may have been underestimated in this study because wing setal damage can be greater for caged parasitoids when compared to conspecifics naturally foraging in the field (Lee et al., 2006). Further research investigating the accuracy of using laboratory-derived wing wear correlations to estimate age of field parasitoids would be useful in determining the reliability of estimates of age and realised lifetime parasitism as presented here.

Heimpel et al. (1998) estimated lifetime fecundity of female *A. aonidiae* in the field using previously attained estimations of pupal mortality rate, adult mortality from predation and the relationship between host size and parasitoid egg load at emergence. Incorporation of techniques used by Heimpel et al. (1998), especially estimates of field observations such as predation rates, egg handling times and encounter rates, may be useful in future studies aimed at refining estimates of the lifetime fecundity of female *G. ashmeadi* in the field.

4.2. Temporal changes in age, egg load and biocontrol potential of field-foraging G. ashmeadi

This study sought to investigate monthly changes in parasitoid age and realised parasitism of living *G. ashmeadi* that were deliberately captured while foraging for *H. vitripennis* egg masses in the field. Based on the assumption that estimated age is correct (and therefore calculated realised parasitism), results suggest that month had a significant effect on age and reproductive output of live parasitoids captured in lemon trees which supports results obtained from collecting dead *G. ashmeadi* falling from nearby orange trees into funnel traps. Estimated initial egg load of *G. ashmeadi* captured in August was four eggs higher than July. This is most likely attributed to differences in female size (females were significantly larger in August) between months because HTL was used to predict initial egg load. Smaller-sized *G. ashmeadi* were observed in July in comparison to August. This size difference could have been due to emergence from eggs of *H. liturata* (Irvin & Hoddle, 2009) because eggs of this species are significantly smaller than *H. vitripennis* (Al-Wahaibi, 2004). Al-Wahaibi and Morse (2010) reported that on citrus trees at UCR Ag. Ops., approximately 33% of eggs laid by *Homalodisca* spp. were *H. liturata* in mid-July compared with approximately 6% in mid-August [the overall season-long average of *H. liturata* egg masses in citrus at Ag. Ops is 10% (Al-Wahaibi & Morse, 2010)].

Some degree of egg limitation is predicted in parasitoid populations (Rosenheim, 1996). Models by Sevenster et al. (1998) predict that even though some successful individuals will lay all their eggs, the majority of individuals become time limited. The vast majority (99.5%) of foraging *G. ashmeadi* captured in this study were time limited. This is in agreement with other studies (Ellers, van Alphen, & Sevenster, 1998; Weisser et al., 1997). Females may possess the ability to decrease oviposition rates when egg loads become limited, thereby reducing the risk of egg limitation (Heimpel et al., 1998; Mangel & Heimpel, 1998). Alternatively, foraging *G. ashmeadi*

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were captured in the early morning and modelling conducted by Casas et al. (2000) predicted that the proportion of parasitoids running out of eggs increases over the course of the day. A study demonstrating that egg load in *A. aonidiae* decreased during the course of the day supports this model (Heimpel & Rosenheim, 1998). Although foraging *G. ashmeadi* in this study were not egg limited, the ovaries of 6% of females contained 1–10 mature eggs suggesting that egg limitation could be possible for a small percentage of females at certain times unless oviposition rates are altered to prevent this (Heimpel et al., 1998; Mangel & Heimpel, 1998).

There was a strong correlation between density of adult *H. vitripennis* and numbers of female *G. ashmeadi* emerging from *H. vitripennis* egg masses which supports 2008 phenology data reported in Hoddle (2010). Interestingly, host egg density was positively correlated with total egg load and number of mature eggs at time of capture. This is in direct contradiction to models predicting that egg limitation occurs more frequently at high host densities (Rosenheim 1996), and may be attributed to egg maturation in *G. ashmeadi* being stimulated by the abundant presence of hosts (Irvin & Hoddle, 2009). Temperature of the previous five days prior to capture was negatively correlated with total egg load and number of mature eggs. This may be attributed to females being more active during higher temperatures and parasitising a higher number of *H. vitripennis* eggs, which decreased egg load. Alternatively, higher temperatures and subsequent heat stress may have slowed or stopped egg maturation, thereby reducing female egg load (Pilkington & Hoddle, 2006). In some instances, temperature may have no significant effect on the egg load of foraging parasitoids (Heimpel & Rosenheim, 1998). Further studies would help improve our understanding of the effects of high temperatures, especially temporary peak maximum temperatures, on parasitoid egg load.

We conclude that, it is likely maximum parasitism of *G. ashmead* is not realised in the field. The majority of females that died from natural causes had mature eggs ready for oviposition which demonstrates that they were time limited with respect to egg laying. Resource subsidisation as part of conservation biological control may enhance the longevity of *G. ashmeadi* thereby increasing the time available to locate and parasitise hosts. Research is required to determine whether deliberate provision of plant resources in the citrus or grapevine ecosystem could enhance biological control of *H. vitripennis* by improving functional ovigeny, longevity and realised fecundity of *G. ashmeadi*.

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