ABSTRACT Aspects of the biology of the adult stage of *Ufens principalis* Owen (Hymenoptera: Trichogrammatidae), an important parasitoid of *Homalodisca* (Hemiptera: Cicadellidae) eggs in southern California, were studied. The field-based sex ratio of *U. principalis* was significantly different from 1:1 and was female biased (62% females). Females and males did not differ significantly in size based on measurements of head width and hind tibia length, and these two variables were highly correlated. There was a significant effect of female age on egg load. Females aged 1, 4, and 5 d had significantly higher egg loads than freshly emerged females. There was also a significant positive linear relationship between egg load and hind tibia length. Egg load averaged 37.9 ± 1.1 eggs. Eggs, which measured 207.8 ± 12.2 μm in length, were elliptical with an anterior nipple-shaped constriction. The longevity of adults was significantly affected by temperature and food (1:1, honey/water). Food had a greater effect in prolonging life as temperature decreased from 35.0 to 10.0°C. The most long-lived adults were fed on honey and kept at 10.0°C (20.2 ± 3.3 d). The rate of parasitism was significantly affected by host age, being significantly higher for 0-h-old eggs than for 12–24-h-old host eggs. There was no significant difference in parasitism between 0- and 0–6-h-old eggs and between 0–6 and 12–24-h-old eggs.

**KEY WORDS** glassy-winged sharpshooter, *Homalodisca vitripennis*, biological control, sex ratio, morphometrics

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) [= *H. coagulata* (Say); Takiya et al. 2006], was introduced into southern California in the late 1980s (or possibly earlier) from its native range in the southeastern United States and northeastern Mexico. It is an important vector of the xylem-limited bacteria, *Xylella fastidiosa* Wells et al., which causes diseases on several crops and ornamentals including Pierce’s disease of grapes, phony peach disease, almond leaf scorch, alfalfa dwarf, and oleander leaf scorch (Blua et al. 1999, UCOP 2000, Varela et al. 2001). The closely related *H. liturata* Ball [= *H. lacerta* (Fowler)] (Burks and Redak 2003), commonly known as the smoke-tree sharpshooter, is native to California and is also a vector of Pierce’s disease and oleander leaf scorch (Freitag et al. 1952, Purcell et al. 1999). Eggs of both *Homalodisca* species are laid just below the epidermis of leaves as a cluster of eggs oriented nearly parallel to one another.

*Gonatocerus* spp. (Hymenoptera: Mymaridae) constitute egg parasitoids acting as regulating biological agents of the egg stage of *Homalodisca* species on woody plants in North America (Turner and Pollard 1959, Huber 1988, Triapitsyn et al. 1998, Triapitsyn 2003, Al-Wahaibi 2004, Owen 2005, Pinto 2006). In addition, Grandgirard et al. (2007) reported that in Tahiti (French Polynesia), egg masses of *H. vitripennis* (which was recently introduced there) were parasitized by *Centrodora* sp. (Hymenoptera: Aphelinidae) as well as by *Palaceoneura* sp. and *Anagrus* sp. (both Hymenoptera: Mymaridae). Other egg parasitoids that may attack *Homalodisca* eggs opportunistically in the Nearctic include *Paracentrobia* spp., *Pseudoligosita* spp., *Oligosita* spp., *Anagrus* spp., and *Ufens* spp. (Hoddle and Triapitsyn 2004, Pinto and Viggiani 2004, Tipping et al. 2005, Krugner et al. 2008). Observations of *Ufens* species (Hymenoptera: Trichogrammatidae) from southern California were made by several workers (Powers 1973, Pinto et al. 1987, Al-Wahaibi and Morse 2000, Morgan et al. 2000, Al-Wahaibi 2004, Al-Wahaibi et al. 2005). Al-Wahaibi (2004) suggested that egg masses of *Homalodisca* on plants native to southern California [e.g., jojoba, *Simmondsia chinensis* (Link) Schneider] were predominantly parasitized by two *Ufens* species, Al-Wahaibi et al. (2005) described, illustrated, and indicated the geographical distributions of these *Ufens* spp. as two new species: *Ufens principalis* Owen and *Ufens ceratus*.
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Owen. The searching, oviposition, emergence, mating, and male competition behaviors of U. principalis were detailed by Al-Wahaibi et al. (2005). The same authors described the emergence, mating, and male competition behaviors of U. ceratus. Of the two Ufens species, U. principalis is the more abundant and more commonly collected species in the city of Riverside in southern California (Al-Wahaibi 2004). A third Ufens species, Ufens simplipes Owen, was described by Owen (2005), as an egg parasitoid of H. liturata in the Coachella Valley, Riverside County. Recently, there has been interest in introducing exotic Ufens species into California as part of a classical biological control effort against the glassy-winged sharpshooter (Triapitsyn and Hoddle 2001, 2002; Triapitsyn et al. 2002). Difficulties in rearing the introduced Ufens species in quarantine lead to the formulation of the hypothesis that Ufens species might be hyperparasitoids attacking Gonatocerus species (primary parasitoids) inside Homalodisca eggs (Triapitsyn 2003). The observations of Al-Wahaibi et al. (2005) of the field oviposition behavior of U. principalis provided the first strong evidence that U. principalis (and probably U. ceratus) is a primary parasitoid of eggs of Homalodisca spp.

Although the biology of the genus Trichogramma is known to a large extent, knowledge of the biology of other genera within the Trichogrammatidae is limited. Despite the important ecological role Ufens species play in the regulation of populations of Homalodisca species, little is known about their biology and ecology. This study is aimed at elucidating aspects of the biology and ecology of U. principalis not covered by Al-Wahaibi et al. (2005). Laboratory studies were conducted with adult wasps to investigate sex ratio, adult morphometrics, egg load, longevity, and parasitism as affected by host age. Such knowledge could assist in designing rearing systems for U. principalis (and possibly U. ceratus) for use in augmentative biological control of Homalodisca species and in the expansion of our understanding of the biology of Trichogrammatidae in particular and egg parasitoids in general.

Materials and Methods

Source of Insects and Rearing Conditions. Ufens parasitized egg masses of Homalodisca used as a source of adult Ufens in experiments were obtained from the field, except for studies requiring lab parasitism. Egg masses of field origin were collected from jojoba in Field 7E, Agricultural Operations, University of California, Riverside, CA, during summer 2002 and spring and summer 2003. Egg masses used as a source of adult Ufens were incubated (inside jojoba leaves) in 9- by 50-mm-diameter tightly closed plastic petri dishes without added within-dish moisture at \( \approx 26.7^\circ C, 50-60\% \) RH, and a photoperiod of 14:10 (L:D) h. Newly emerged Ufens adults in incubation dishes were dislodged by tapping opened dishes over a white sheet of paper. They were then collected by placing a 1-dram glass vial over the adult on the sheet of paper, i.e., as they moved upward, they were trapped by taking advantage of their positively phototactic behavior.

Sex Ratio of Field-Parasitized Egg Masses. The field sex ratio of U. principalis was determined from egg masses collected on jojoba in early April and early August 2003. The egg masses were incubated (as described above) and checked daily for U. principalis emergence. After 3 d of initial emergence (based on observation by Al-Wahaibi 2004 that \( \approx 90\% \) of adults complete emergence within the first 3 d after emergence begins), the egg masses inside the rearing containers were frozen and were then assessed within a week of freezing. Adult U. principalis were sexed by examination through a dissecting microscope and were recorded on a per egg mass basis. The characteristics of the antennae (longer antennal flagellum and longer, bushier antennal setae in males) and genitalia (ovipositor present in females) were used to distinguish the sexes. The proportions of females per egg mass for spring and summer populations were compared using a \( t \)-test after arc sine transformation of the data. To determine whether numbers of the two sexes were equal, a goodness-of-fit chi-square test (to an expected ratio of 1:1) was used.

Adult Morphometrics. To obtain a preliminary estimate of the variation in size of adult U. principalis and compare male and female sizes, 20 males and 20 females were randomly sampled by 1) trapping \( >40 \) emerged adults, each in a small glass vial; 2) placing these vials in a container; and 3) removing vials from the container by lottery without replacement until a total of \( 20 \) males and \( 20 \) females were obtained out of a population that originated from jojoba and emerged in late September 2003. Two variables were used as measurements of size, namely hind tibia length and head width, because of their use in parasitic Hymenoptera research as good predictors of adult parasitoid size (Jervis and Copland 1996). Insects were measured in the afternoon on the day of emergence after complete sclerotization of the integument. Each measured individual was placed in a drop of 1:1 honey/water mixture on a microscope slide by using a fine brush. The viscous honey/water mixture was used because it held the insect firmly in position better than did water. Using a fine insect pin, the head of the insect was severed from the rest of the body. Then, the head and the body, with the legs attached, were transferred to a drop of water on a clean microscope slide. The head was placed in the drop of water with its posterior side down. A coverslip was placed gently over the head and body so as to not break or distort the head. After measuring the head width, pressure was applied on the cover slip until the body and legs were flattened and approximately parallel to the surface of the cover slip; then the hind tibia length was determined. Both structures were viewed through a compound microscope and measured at 150\( \times \). A micrometer within the ocular lens of the microscope was used to measure lengths. Head width was the maximum distance between the outer margins of the two compound eyes. Hind tibia length was measured from the middle of the joint between the hind femur and hind tibia to the apical margin of the tibia. Hind tibia length and head width were compared between females and males.

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using t-tests. Correlation and linear regression analyses of the two variables were conducted for each sex separately and for all data pooled for the two sexes.

**Egg Load Versus Female Age and Size.** Newly emerged *U. principalis* females from field-parasitized egg masses on jojoba were collected in 1-dram vials containing droplets of 1:1 honey/water mixture. These females were collected in the morning on two consecutive days in late September 2003. Most females emerged during the morning (0600–1200 hours; Al-Wahaibi 2004). Each daily cohort was divided into six age groups: 0, 1, 3, 4, 5, and 20 d old. This was done by setting aside 10 randomly selected females on each of two days for each of the six age groups (six age groups × 2 d × 10 females = 120 total). The 0-d-old group was assessed for egg load and size on the day of emergence. Females destined for other age groups were left to stand at room temperature (24°C), 50% RH, and a photoperiod of ~13:11 (L:D) h until reaching the appropriate age, and then they were assessed for egg load and size of the female. All assessments of egg load and female size were done between 1100 and 1300. Twenty females were used for each of the age groups except for the 20-d age treatment for which only 13 females were assessed because of low survivorship to that age. On reaching the appropriate age, each female was transferred into a drop of water on a microscope slide by using a fine brush. A coverslip was then gently placed over the insect. Pressure was applied to the cover slip (using the base of the brush) to tear the abdomen of the insect allowing eggs within the abdomen to flow out into the surrounding water. Enough pressure was applied to allow exit of all or most eggs from the body cavity without crushing the specimen. As much as possible, pressure was applied carefully so as not to cause the eggs to spread throughout the area under the cover slip, making it difficult to find all eggs. In addition, the morphology of the eggs was noted and egg lengths and widths were measured for 10 eggs from a single, typical, freshly emerged female. Egg dimension measurements were made after allowing the eggs to fully inflate in the water surrounding the specimen. Eggs were observed, counted, and measured at 150×. After the eggs were counted, the length of one of the hind tibia of each examined female was measured as an index of female size (Jervis and Copland 1996), as described above except that measurements were done at 675× to improve precision. Egg load (number of eggs per female) was regressed against hind tibia length using linear regression. The effect of female age on egg load was tested using one-way analysis of variance (ANOVA) by considering female age to be a discrete categorical variable.

**Longevity of Adults.** This experiment tested the effect of temperature, food, and sex on the longevity of adult *U. principalis*. The design consisted of three temperature levels (10.0, 26.7, and 35.0°C), two food levels (fed on honey and unfed), and two sex levels (male and female), making up 12 treatments that were studied using a completely randomized design. Each treatment was replicated 20 times (n = 240 in total). Newly emerged adults originated from egg masses obtained on the same date from jojoba. Adults were collected in the morning in 1-dram glass vials either treated with a streak of small droplets of 1:1 honey/water solution or were untreated. Females and males were assigned randomly to treatments and vials containing adults were held vertically inside cardboard cells. Vials inside cardboard cells were placed inside Percival growth chambers (Percival Scientific, Inc., Perry, IA) at 10.0, 26.7, and 35.0°C (actual mean temperatures as measured using HOBO data loggers, Onset Computer Co., Bourne, MA), and at 30% RH and a photoperiod of 14:10 (L:D) h. Vials were checked daily in the evening for survivorship of adults, which were scored as dead if they were not firmly attached to the vial wall and if they did not display movement of legs, wings, antennae, or the head. Adults that died via entrapment in honey/water droplets were excluded from the assessment and were replaced with newly emerged adults. The date of death was recorded and longevity was determined as the number of days between emergence and death. A three-way ANOVA was conducted to determine the significance of the main factors (temperature, food, and sex) and all possible interactions. Means of significant main effects were compared using one-way ANOVA and Tukey’s Honestly Significant Difference (HSD) procedure or t-tests.

**Effect of Host Egg Mass Age on Parasitism.** Three host egg mass age groups were created for this experiment: 0, 0–6, and 12–24 h old. These represent the initial ages of host egg masses at the time of first exposure to *U. principalis* females. Egg masses were produced by *H. vitripennis* females collected from Fields 7F, 7G, and 7H at Agricultural Operations, University of California, Riverside. The 0-h-old host age group was produced by introducing 8–10 *U. principalis* females, 2–5 min after three *H. vitripennis* females were released inside clear plastic cylindrical cages (8 cm in diameter by 15.5 cm in height) placed over 2–3 mo-old jojoba seedlings. To produce some egg masses (usually 1–3) on each jojoba seedling, this number of sharpshooters was deemed sufficient without causing sufficient feeding damage that might lead to death of the plants. The 0–6-h-old host age group resulted from releasing eight to 10 *U. principalis* females inside the same cylindrical cages on jojoba seedlings containing egg masses produced by exposing these seedlings during the previous 6 h to a large number of *H. vitripennis* females in a sleeve cage. The 12–24-h-old host age group was set up by leaving a large number of *H. vitripennis* to oviposit on jojoba seedlings inside a sleeve cage for 12 h (morning to night) and then incubating plants infested with egg masses (but free of *Homalodisca* adults and *Ufens*) for another 12 h. At the end of the second 12-h period, eight to 10 *U. principalis* females were released inside the cylindrical cage covering the egg mass-infested jojoba seedlings. For both the 0–6- and 12–24-h treatments, the range of number of egg masses exposed to *U. principalis* was one to three per plant. The three host age treatments were tested simultaneously for parasitism on the same day.
The experiment was replicated on a number of days until sufficient numbers of egg masses were produced as replicates for analysis. *U. principalis* were exposed to the three host age groups for 24 h in a growth chamber (at 26.7°C, 30% RH, and a photoperiod of 14:10 [L:D]; see details above). After exposure, the cage was removed and any *U. principalis* were shaken off the plant. Plants containing *Homalodisca* egg masses (some plants in the 0-h treatment and all plants in the 0–6- and 12–24-h treatments) were then incubated under the same conditions as used above during exposure to *U. principalis* females. Each egg mass was incubated until 1 wk after initial emergence of either *H. vitripennis* nymphs or *U. principalis* adults. For the three host age treatments, the number of parasitized eggs (per egg mass) was recorded for each egg mass. One-way ANOVA was used to test for the effect of host age on rate of parasitism (determined as the proportion of parasitized eggs). Tukey’s HSD procedure was used for pairwise mean comparisons.

**Statistical Software.** Chi-square tests, *t*-tests, one-way ANOVAs, multiway model fitting, mean comparisons descriptive statistics, and linear regressions were conducted using JMP IN (SAS Institute 1996).

**Results**

**Sex Ratio of Field-Parasitized Egg Masses.** There was no significant difference (*P* = 0.6701; *n* = 80, 114) in the proportion of *U. principalis* females per egg mass between the spring (0.63 ± 0.02 [SEM]) and summer (0.62 ± 0.01) parasitoid populations collected on Riverside jojoba. The proportion of females per egg mass (combined spring and summer populations) was 0.62 ± 0.01. The ratio of females to males was significantly different from 1:1 as determined by a chi-square test (combined spring and summer populations, *χ²* = 330.4, *P* < 0.0001; df = 1, *n* = 194). A low percentage of egg masses resulted in 100% male progeny (2.5 and 0.8%, respectively, for spring and summer 2003).

**Adult Morphometrics.** Female and male *U. principalis* did not differ significantly in head width (*t*-test, *P* = 0.123; *n* = 20 for both sexes). Mean female head width was 306.3 ± 8.6 μm (SEM). Males averaged 289.3 ± 6.5 μm in head width. In terms of hind tibia length, the two sexes also did not differ significantly (*t*-test, *P* = 0.0849; *n* = 20 for both sexes). Female hind tibia length measured 178.3 ± 4.8 μm on average, whereas male hind tibia length was 168.6 ± 2.7 μm. Hind tibia length (x) and head width (y) of all insects were highly correlated (*r* = 0.845, *P* < 0.0001; *n* = 40). This correlation between the two indices of size was stronger for females (linear regression, *y* = 1.5395x + 21.92; *r* = 0.890, *P* < 0.0001; *n* = 20) than for males (*y* = 1.770x − 9.034; *r* = 0.730, *P* = 0.0003; *n* = 20).

**Egg Load Versus Female Age and Size.** There was a significant effect of *U. principalis* female age on egg load (one-way ANOVA, *P* = 0.0008; *n* = 113). Egg loads of females 1-d-old and older were numerically higher than the egg loads of 0-d-old females, with females 1, 4, and 5 d old showing significantly higher egg loads than 0-d-old females (Fig. 1). However, there was a significant positive linear relationship between *U. principalis* egg load and hind tibia length (*r* = 0.624, *P* < 0.0001; *n* = 113). Figure 2 shows a plot of this relationship and provides a linear regression equation Egg load of *U. principalis* averaged 37.9 ± 1.1 eggs (range, 8–73; *n* = 113), whereas hind tibia length averaged 178.3 ± 1.7 μm (range, 136.4–223.3; *n* = 113).

**Figure 3, A and B, shows eggs of *U. principalis* dissected out of the female’s body and a close-up of one egg. Eggs of *U. principalis* were elliptical in shape with one end rounded and the other end distinctly nipple-shaped (i.e., the end of the egg was narrow and constricted; Fig. 3B). Eggs of *U. principalis* seemed flatter and narrower when first released from the female’s abdomen and inflated on contact with water to the full shape described above. Egg length averaged 207.8 ± 12.2 μm (range, 155.6–255.0; *n* = 10), whereas the average egg width was 69.6 ± 4.0 μm (range, 51.0–86.7; *n* = 10). The mean egg nipple length (measured from apex to base) was 19.4 ± 3.3 μm (range, 10.2–28.1; *n* = 5).
Longevity of Adults. Based on the three-way ANOVA relating the effect of temperature, food, and sex on longevity, only the main effects of temperature \((P < 0.0001, \text{df} = 2; n = 240)\) and food \((\text{df} = 1, P < 0.0001)\) significantly affected *U. principalis* adult longevity. Among the interactions, only that between temperature and food was also significant \((\text{df} = 2, P < 0.0001)\). One-way ANOVAs were therefore conducted to test for the effect of temperature at each of the two food levels (honey and no honey), and *t*-tests were used to test the effect of food at each of the three temperature levels \((10.0, 26.7, \text{and} 35.0^\circ \text{C})\). All one-way ANOVAs and *t*-tests were highly significant \((all P < 0.0001)\). Figure 4 shows comparisons of mean longevity versus levels of temperature and food and how they interacted with one another. Note that as temperature increased, the difference in longevity owing to the availability of food became smaller, in other words, food had a greater effect in prolonging life when food was provided. The most long-lived adults were males fed on honey that were kept at 10.0°C \((20.2 \pm 3.3 \text{ d})\) and the most short-lived adults were either males or females not fed honey and kept at 35.0°C \((1.0 \pm 0.0 \text{ d})\) (Table 1).

Effect of Host Egg Mass Age on Parasitism. Although the rate of parasitism was generally low for all three host age groups evaluated in this experiment, the rate of parasitism by *U. principalis* was significantly affected by host age (ANOVA, \(P = 0.0366; n = 18–60\)). Rate of parasitism of 0-h-old eggs was significantly higher than for 12–24-h-old host eggs. There was no significant difference in parasitism between 0-h- and 0–6-h-old eggs and between 0–6- and 12–24-h-old eggs (Fig. 5).

Discussion

Sex Ratio of Field-Parasitized Egg Masses. The sex ratio of *U. principalis* as determined from field-parasitized egg masses was female biased (62% in both
spring and summer 2003). This sex ratio is substantially lower than that reported for the related trichogrammatid Zagella delicata De Santis (79%, field-collected; Logarzo et al. 2004). A female-biased sex ratio was also reported by Virla 1999, in Logarzo et al. 2004) for Paracentrobia sp., another trichogrammatid. Female-biased sex ratios seen in the current study are typical of gregarious Trichogramma spp. attacking large hosts (e.g., Hamilton 1967, Lagace 1998, Babendreier et al. 2003).

The sex ratio of the closely related species *U. ceratus* tended to be more female-biased. This was especially the case for *U. ceratus*-parasitized egg masses on jojoba from Desert Center, CA, where 75% of adults were females (Al-Wahaibi 2004). *U. ceratus* was generally less abundant than *U. principalis* on jojoba in Riverside (Al-Wahaibi 2004). In Desert Center, densities of *U. ceratus* were even lower than in Riverside, due to the generally lower parasitism rates in Desert Center jojoba combined with lower Homalodisca egg mass densities relative to Riverside (Al-Wahaibi 2004).

Schmidt (1994) stated that for most *Trichogramma* species, as host patch size (host egg clutch size) increases, sex ratio becomes increasingly female-biased. Because *H. vitripennis* eggs (the predominant host species present) attacked by *U. principalis* are laid in clutches of 8.5 eggs per egg mass on average and could reach as many as 30 eggs per egg mass (Al-Wahaibi 2004), it is not surprising, based on Schmidt’s (1994) statement, that *U. principalis* adult populations are generally female-biased. However, an increase in the number of *U. principalis* females visiting and ovipositing in host egg patches (such as that observed in summer in Riverside; see above) would be expected to decrease the likelihood of sib-matings and increase the chance of hybridization and gene flow within the population. This could be advantageous to the continuation and fitness of *U. principalis* as a species.

As in most Trichogramma species and indeed most Hymenoptera (Schmidt 1994), *U. principalis* is arrhenotokous, producing both sexes in normal cases and only in cases where females are unmated, do they produce solely male progeny. A low percentage of egg masses parasitized by *U. principalis* produced solely males (1–3%). This suggests that relatively few *U. principalis* females were unmated and attests to the highly successful mating system in this species, probably because mating is accomplished immediately after female emergence from the egg mass (Al-Wahaibi et al. 2005), thus reducing the need for males to locate females away from emergence sites. Long-distance mate location is hypothesized to occur more frequently in solitary parasitoid species attacking solitary host eggs (not in masses) and probably is characterized by higher levels of virgin females than in the gregarious system of *U. principalis*. This in turn, is expected to result in females producing more male progeny, which would drive sex ratios close to the unbiased 0.5 level. Waage (1986) stated that sex ratios in solitary Hymenoptera attacking dispersed hosts (those not found in groups) tended to be near a sex ratio of 0.5 or were slightly female-biased.

### Table 1. Descriptive statistics for the longevity of adult *U. principalis* under 12 treatment regimes involving combinations of three temperatures, food level (honey, no honey), and sex

| Temp. (°C) | Food | Sex     | Mean  | SEM  | Min. | Max. | n  |
|-----------|------|---------|-------|------|------|------|----|
| 10.0      | Honey| Female  | 19.20 | 3.29 | 2    | 47   | 20 |
| 10.0      | Honey| Male    | 20.20 | 1.96 | 5    | 34   | 20 |
| 10.0      | No honey | Female  | 5.80  | 1.02 | 1    | 16   | 20 |
| 10.0      | No honey | Male    | 5.15  | 0.53 | 1    | 10   | 20 |
| 26.7      | Honey| Female  | 9.00  | 1.23 | 2    | 23   | 20 |
| 26.7      | Honey| Male    | 6.85  | 0.98 | 2    | 14   | 20 |
| 26.7      | No honey | Female | 1.38  | 0.18 | 1    | 4    | 20 |
| 26.7      | No honey | Male | 1.65  | 0.23 | 1    | 5    | 20 |
| 35.0      | Honey| Female  | 2.75  | 0.35 | 1    | 6    | 20 |
| 35.0      | Honey| Male    | 2.35  | 0.39 | 1    | 8    | 20 |
| 35.0      | No honey | Female | 1.00  | 0.00 | 1    | 1    | 20 |
| 35.0      | No honey | Male | 1.00  | 0.00 | 1    | 1    | 20 |
Adult Morphometrics. There was considerable variation in the size of *U. principalis* females and males, with the largest specimens ≈50% larger than the smallest specimens. Females did not differ in size (based on head width and hind tibia) from males. The highly gregarious habit of *U. principalis* (especially for parasitized egg masses in late summer) and the high variation in the number of parental females ovipositing in egg masses (see discussion above) are two factors probably responsible for the substantial variation in adult size and the inability to detect a difference in size between males and females. The strong correlation between head width and hind tibia length, both commonly used indices for parasitoid adult size (Jervis and Copland 1996), suggests that both variables can be reliably used as proxies for adult size in *U. principalis*.

Egg Load Versus Female Age and Size. Eggs of *U. principalis* are sausage-shaped with a peduncle (nipple) at the anterior end. The eggs of *U. principalis* and *U. ceratus* (A.K.A., unpublished data) are similar in general shape although *U. principalis* tended to have longer and narrower egg nipples. This shape stands in contrast to the general shape of eggs of *Trichogramma* species pictured by Clausen (1940) who described them as “somewhat elongate, with the middle portion distinctly expanded, and both ends are smoothly rounded.” The difference between egg shape of *Trichogramma* and *Ufens* spp. lies in the lack of a peduncle or nipple in *Trichogramma* eggs and the generally less elongate shape of *Trichogramma* eggs. *Ufens* egg shape is also different from the relatively bizarre shape of eggs of *Poropoea* sp. (Trichogrammatidae) that have a tail-like structure on one end of the egg and a handle-like structure on the other end as described and illustrated in Clausen (1940). However, eggs of *Ufens* are similar in shape to what has been reported for other trichogrammatids such as *Pseudoligosita krygeri* (Girault) (Bakkendorf 1934, then *Chaetostricha pulchra* Kryger), *Pseudoligosita utilis* (Kowalski) (Taylor 1937, then *Oligosita utilis* Kowalski), *Paracentrobia andoi* (Ishii) (Vungsilabutr 1978), and *Lathromeris cecidomyiidae* Viggiani & Laudonia (Jesu and Laudonia 1997).

*U. principalis* exhibited characteristics of both proovigenic and synovigenic parasitoids. It had a relatively high complement of eggs upon emergence and this egg complement increased as females reached 24-h-old and then remained relatively constant with increasing female age, even at the advanced age of 20 d. Jervis and Copland (1996) stated that proovigeny and synovigeny are not discrete categories but are states of egg production that can vary on a continuum from one species to another. Moreover, they mentioned that the majority of parasitoids are synovigenic, and that “among insects there are varying degrees of synovigeny.” Trichogrammatids, represented by *Trichogramma* species, have in the past been considered good examples of proovigenic parasitoids (Waage and Ming 1984), Bai et al. (1992) due to their relatively short life, general lack of host-feeding, and their possessing a large egg complement shortly after adult emergence. However, there is evidence that some trichogrammatids deviate from this general pattern. Henriquez and Spence (1993) noted a resurgence in the oviposition of *Lathromeroidea* sp. on the seventh day postexposure to hosts after a general decline in parasitism from the second to the sixth day postexposure. More recently, Mills and Kuhlmann (2000) argued, based on their own research and research by others (Houseweart et al. 1983, Bai and Smith 1993), that many *Trichogramma* species are indeed synovigenic, maturing eggs throughout their adult life.

Given there was no significant difference among egg loads of 1–5-d-old females, whereas 0-d-old females had a significantly lower egg load than 1-d-old females, one can hypothesize that *U. principalis* females reach a maximum egg load one day after emergence (as is also the case with *Trichogramma platneri* Nagarkatti; Mills and Kuhlmann 2000). This may result in 1-d-old *U. principalis* females searching more eagerly and being more responsive to host cues to reduce parasitism.
their egg load. This responsiveness may be lost to some degree as females age beyond 1 d old. Many researchers dealing with the biology of Trichogramma produced experimental data indicative of a decrease in parasitism when female parasitoids were >1 d old. Hoffmann et al. (1995) showed that parasitism by Trichogramma ostriniae Pang & Chen, provided with honey continuously, dropped rapidly as females aged from 1 to 5 d old, and then remained at relatively low and stable levels until 17 d of age. Mills and Kuhlmann (2000) presented data for three Trichogramma species that showed oviposition peaking one day after emergence, then decreasing, and remaining at fairly constant but low levels from days 2 to 11. Similarly, Takada et al. (2000) reported that parasitism by Trichogramma dendrolimi (Matsumura) (measured as the number of emerged progeny) was highest for 1-d-old females, which along with 2-d-old females, produced significantly higher parasitism than 3–5 d-old females. It is expected that with age, female trichogrammatids may tend to deplete their supply of eggs and may or may not develop more eggs. Such depletion would result in a drop in the rate of parasitism observed as females age.

However, linking the temporal variation of egg load and lifetime fecundity of U. principalis can only be assessed with experiments that examine the daily oviposition rates of single U. principalis females for their whole life span and that follow changes in egg load with female age for a cohort of females provided with host eggs. Without such experiments, it is difficult to draw definite conclusions regarding the egg production strategy of U. principalis (i.e., where it is on the synovigeny scale) and whether oviposition rates are indeed maximal early in the life of the female (i.e., at 0–1 d old). Data of this nature could be useful in the selection of the most effective U. principalis female age (i.e., that with a maximal oviposition rate) to be used in laboratory experiments, mass rearing, and releases in the field.

Based on the current study, it can be concluded that egg load shows a significant positive linear relationship with the size of females, as estimated using the length of the hind tibia. Similar results have been reported in several studies with Trichogramma species (Hohmann et al. 1988, Pavlik 1993, Mills and Kuhlmann 2000). However, Mills and Kuhlmann (2000) cautioned against using egg load as a proxy for fitness and potential fecundity of parasitoids because the Trichogramma they examined continued to develop eggs throughout their life, ultimately reaching fecundity levels beyond their egg load when they were 24 h old. Hence, they argued that a direct relationship between the size of the female and fitness within and among species cannot be assumed. However, Ruberson and Kring (1993) stated that the size of female Trichogramma pretiosum Riley (based on the length of the hind tibia) showed a significant positive linear relationship with lifetime fecundity and daily oviposition rate.

**Longevity of Adults.** According to Jervis and Copland (1996), temperature is negatively correlated with longevity within the optimum range of survival for many parasitoid species. U. principalis seemed to follow this model relating longevity to temperature. However, Vungsilabutr (1978) reported that when provided with honey, Paracentrobia andoi lived 15.9 d at 25°C versus 11.1, 11.2, and 1.1 d at 15, 20, and 30°C, respectively. This contrasts with U. principalis surviving the longest at the lowest temperature of 10.0°C when fed honey (Table 1). This disparity could be due to a higher intolerance of P. andoi versus U. principalis to low temperatures. Comparison with data by Vungsilabutr (1978) suggests that U. principalis lives longer than P. andoi at warm temperatures (2.6 d at 35.0°C for U. principalis versus 1.1 d at 30°C for P. andoi). This tolerance to both heat and cold indicates that U. principalis, a native to southern California inland valleys and desert areas, is apparently adapted to extremes in temperatures typical of dry areas (deserts). Data provided by Awadalla (1996) for Monorthochaeta nigra Blood & Kryger (Trichogrammatidae) indicate that the longevity of this species was negatively associated with temperature in the range of 20–30°C and that its longevity at warm temperatures was midway between that of U. principalis and P. andoi (2.4 d at 30.0°C).

The current study provides evidence that U. principalis adults fed on honey survived significantly longer than unfed adults held at the same temperature. This result is consistent with reports in the literature indicating that many parasitoids live longer when given a diet rich in carbohydrates versus when starved or provided water alone (Jervis and Copland 1996). It is not known whether U. principalis adults feed in the field. Jojoba, as the source of U. principalis used in this experiment, has no apparent nectaries and the flowers (probably not a good nectar source) are restricted temporarily to late winter and early spring (Thomson 1982), a time when U. principalis parasitism was generally low (Al-Wahaibi 2004). Very few honeydew-producing insects feed on jojoba based on the faunal survey by Pinto et al. (1987) and our observations (A.K.A.). Thus, it is likely that U. cfens is short-lived in the field, especially in the summer. However, it is possible that adults disperse to feed on nectar or honeydew on plants such as citrus in the vicinity of jojoba. It is expected that the longevity of U. principalis females, not provided with hosts in the current study, could have been lower had they been given the chance to oviposit. Hoffmann (1999) found greater longevity in trichogrammatid species he studied when hosts were not provided. However, Lund (1938), cited in Clausen (1940) stated that the longevity of Trichogramma evanescens Westwood was not affected by the unavailability of host eggs for 2–3 d. Generally, female trichogrammatids live longer than males under the same rearing conditions. In the current study, there was no significant difference in longevity between female and male U. principalis. Logarzo et al. (2004) reported that females of Z. delicata lived significantly longer than males (12.2 and 6.2 d, respectively, at 24.5°C). Taylor (1937) stated that females of P. utilis lived longer than males but he did not provide statistical comparisons for the two sexes. Similarly, Gonzalez-Va Zena zuela and Estrada-Ortiz (1983) indicated greater longevity for females of Brachyufens.
osborni Dozier (Trichogrammatidae) over males but did not test whether this difference was significant. Data obtained on longevity in the current study could be applicable to the design of cold storage (around 10°C) protocols for *U. principalis* in future experiments. One question that might be addressed in future studies is the effect of cold storage on the fitness of *U. principalis* females and their parasitism efficiency once they are removed from storage.

**Effect of Host Egg Mass Age on Parasitism.** Al-Wahaibi et al. (2005) stated that *U. principalis* females in the field parasitized *Homalodisca* eggs on jojoba within minutes of their being laid, and parasitism apparently ceased approximately an hour after arrival of the first *U. principalis* female on the egg mass. Data from laboratory experiment in the current study corroborated these field observations. In the laboratory, significantly higher parasitism was observed on eggs that were laid by *H. vitripennis* concurrent with the presence of female *U. principalis* (0-h-old eggs) than on host eggs that were 12–24-h-old before exposure to *U. principalis* females (none of the 12–24-h-old host eggs were parasitized by *U. principalis* females). However, host eggs of intermediate age (0–6 h old) were parasitized to a lower degree than 0-h-old host eggs, but this difference was not statistically significant. This lack of significance could be due to some of the 0–6-h-old eggs being very young, perhaps as young as the 0-h-old eggs, when they were exposed to *U. principalis*. A second possibility is that parasitism rates for the two host age groups were generally not high enough to detect statistical differences.

Even though the present experiment investigating the effect of host age was based on a no-choice design, *U. principalis* females did not attack 12–24-h-old eggs they were exposed to within the same cage. We believe such eggs were probably just as suitable as 0-h-old and 0–6-h-old eggs for development of *U. principalis* immatures (tissues in *H. vitripennis* eggs start to differentiate at ~90 h at 25°C; Al-Wahaibi 2004). A hypothesis for the lack of attack on 12–24-h-old eggs is that odors associated with freshly laid *Homalodisca* eggs (from sharpshooter accessory glands secretions and/or leaf injury) may dissipate rapidly (within minutes to an hour) making eggs older than ~1 h virtually unattractive to and/or undetectable by *U. principalis* females.

Other trichogrammatids reported in the literature are not as host age-restricted as *U. principalis*. After reviewing the literature on host age selection by *Trichogramma* spp. on 28 host egg species, Pak (1986) concluded that there was no consistent pattern for host age selection among the different combinations of *Trichogramma* and host species. In most of these combinations, host age groups were parasitized to the same degree; young (0–2-d-old) and medium-aged hosts (intermediate between young and old) were preferentially parasitized versus old host eggs (0–2 d before hatching), or parasitism decreased proportionate with an increase in host age. Cases where parasitism was restricted to young host eggs (as in the case of *U. principalis*) made up 10% of 49 parasitism cases that Pak (1986) looked at. According to Godin and Boivin (2000), 67% of 42 *Trichogramma* and *Trichogrammatoida* strains exposed to young, medium-aged, and old host eggs showed a preference for young *Triophasia ni* (Hübner) (Lepidoptera: Noctuidae). The remaining strains (33%) did not show a preference for any of the host age classes. Godin and Boivin (2000) also indicated that the response of the 42 strains they used depended on the host species, as only 17 and 29% of these strains displayed preference for young hosts of *Fieris rapae* (L.) (Lepidoptera: *Fieri- dae*) and *Plutella xylostella* (L.) (Lepidoptera: *Plute- llidae*), respectively. One good example of a *Tri- chogramma* species that apparently prefers very young eggs is *T. dentrolimni* (Takada et al. 2000). Also, Liu et al. (1998) found that parasitism of the host eggs of *Ostrinia furnacalis* (Guenee) (Lepidoptera: Pyralidae) was highest on 0–6-h-old eggs (48%), with parasitism of 18–24-h-old host eggs drastically reduced (22%).

The literature provides little information on the effect of host age on parasitism by trichogrammatid genera other than *Trichogramma*. Taylor (1937) reported that *Psudoligosita utilis* attacked eggs of any age although it showed a preference for recently laid eggs. *Uscana mukerjii* (Mani) produced maximal parasitism on 0–24-h-old host eggs (Kapila and Agarwal 1995).

In the current study, *U. principalis* was shown to parasitize egg masses of *Homalodisca* sp. in the laboratory in the absence of other parasitoids. Moreover, consistent with the field data of Al-Wahaibi et al. (2005), *U. principalis* restricted its parasitism to very young host eggs probably because of attraction to host-related odors associated with freshly-laid egg masses. Data from the current study confirm one of the conclusions of Al-Wahaibi et al. (2005), i.e., that *U. principalis* is not a hyperparasitoid as was initially suspected (Triapitsyn 2003) because of difficulties in rearing (Triapitsyn and Hoddle 2001, 2002; Triapitsyn et al. 2002). Future rearing protocols for *U. principalis* should be based on concurrently caging females of this parasitoid with gravid *Homalodisca* females, thereby providing very young eggs to *U. principalis* females. Cage design and rearing setup should take into consideration an optimal cage size and shape to enhance the detection of volatile host-related odors. Rearing conditions should also be set to enhance the volatility of host-related odors and to optimize the activity of foraging *U. principalis* females. It is expected that a warm, dry, and low-to-medium light regime inside relatively small odorless cages would help optimize parasitism by *U. principalis* in the laboratory.

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References Cited

Al-Wahaibi, A. K. 2004. Studies on two Homalodisca species (Hemiptera: Cicadellidae) in southern California: biology of the egg stage, host plant and temporal effects on oviposition and associated egg parasitism, and the biology and ecology of two of their egg parasitoids, Ufens A and Ufens B (Hymenoptera: Trichogrammatidae). Ph.D. dissertation, University of California, Riverside.

Al-Wahaibi, A. K., and J. G. Morse. 2000. Oviposition of Homalodisca species (Hemiptera: Cicadellidae) and associated egg parasitoids on citrus: cultivar effects, p. 101. In M. S. Hoddle [ed.], Proceedings, California Conference on Biological Control, 11–12 July 2000, Riverside, CA. College of Natural and Agricultural Sciences, University of California, Riverside, CA.

Al-Wahaibi, A. K., A. K. Owen, and J. G. Morse. 2005. Description and behavioural biology of two Ufens species (Hymenoptera: Trichogrammatidae) egg parasitoids of Homalodisca species (Hemiptera: Cicadellidae) in southern California. Bull. Entomol. Res. 95: 275–288.

Awadalla, S. S. 1996. Biological studies on Monorthochaeta nigra Blood & Kryger (Hym, Trichogrammatidae) as egg parasitoid of Centrodora sp. (Col, Chrysomelidae). J. Appl. Entomol. 120: 353–355.

Babendreier, D., S. Kuske, and F. Bigler. 2003. Biological investigations on some Monarchocheta species (Hemiptera: Cicadellidae) reared from eggs of the cabbage looper and the Angoumois grain moth, with and without access to honey. J. Econ. Entomol. 1: 1307–1–310.

Bai, B.R., R. F. Luck, L. Forster, B. Stephens, and J.A.M. Southard. 1988. The life cycle, pp. 63–161. In M. Jervis and N. Kidd, [eds.], Insect natural enemies: practical approaches to their study and evaluation. Chapman & Hall, London, United Kingdom.

Bai, B., and S. M. Smith. 1993. Effect of host availability on reproduction and survival of the parasitoid wasp Trichogramma minutum. Ecol. Entomol. 18: 279–286.

Bai, B. R., R. F. Luck, L. Forster, B. Stephens, and J.A.M. Janssen. 1992. The effect of host size on quality attributes of the egg parasitoid, Trichogramma pretiosum. Entomol. Exp. Appl. 64: 37–48.

Bakendorf, O. 1993. Biological investigations on some Danish hymenopterous egg parasites, especially in homopterous eggs, with taxonomic remarks and descriptions of new species. Entomol. Forening. Cph. 19: 1–134.

Blua, M. J., P. A. Phillips, and R. A. Redak. 1999. A new sharpshooter threatens both crops and ornamentals. Calif. Agric. 53: 22–25.

Burks, R. A., and R. A. Redak. 2003. The identity and reinstatement of Homalodisca liturae Ball and Phera lacerta Fowler (Hemiptera: Cicadellidae). Proc. Entomol. Soc. Wash. 105: 674–678.

Clausen, C. P. 1940. Entomophagous insects. McGraw-Hill, New York.

Freitag, H. H., N. W. Frazier, and R. A. Fleck. 1952. Six new leathvectors of Pierce’s disease virus. Phytopathology 42: 533–534.

Godin, C., and G. Boivin. 2000. Effects of host age on parasitoid and progeny allocation in Trichogrammatidae. Entomol. Exp. Appl. 97: 149–160.

Gonzalez-Valenzuela, M., and J. Estrada-Ortiz. 1983. Longevity and capacity parasitica de Ufens osborni y Tetrastichus haitiensis, parasitos de huevo de Pachnaeus litus. Sci. Agric. (Cuba) 14: 51–56.

Grandirard, J., M. S. Hoddle, S. V. Triapitsyn, J. N. Petitti, G. K. Roderick, and N. Davies. 2007. First records of Gonatocerus dolichocerus Ashmead, Palaemonura sp., Anagrus sp. (Hymenoptera: Mymaridae), and Centrodora sp. (Hymenoptera: Aphelinidae) in French Polynesia, with notes on egg parasitism of the glassy-winged sharpshooter, Homalodisca vitripennis (Germar) (Hemiptera: Cicadellidae). Pan-Pac. Entomol. 53: 177–184.

Hamilton, W. D. 1967. Extraordinary sex ratios. Science (Wash., D.C.) 156: 477–488.

Henriquez, N. P., and J. R. Spence. 1993. Studies of Lathromeroidea sp-nov (Hymenoptera, Trichogrammatidae), a parasitoid of gerrid eggs. Can. Entomol. 125: 693–702.

Hoddle, M. S., and S. V. Triapitsyn. 2004. Searching for and collecting egg parasitoids of glassy-winged sharpshooter in the central and eastern USA, pp. 342–344. In M. A. Tarti, Oswalt, S. P. Blnco, A. Ba, T. Lorik, and T. Esse [eds.], Symposium Proceedings, 2004 Pierce’s Disease Research Symposium, 7–11 December 2004, San Diego, CA. Copeland Printing, Sacramento, CA.

Hoffmann, M. P., D. L. Walker, and A. M. Shelton. 1995. Biology of Trichogramma ostriniae (Hym: Trichogrammatidae) reared on Ostrinia nubilalis (Lep.: Pyralidae) and survey for additional hosts. Entomophaga 40: 387–402.

Hohmann, C. L. 1999. Somatic-gametic tradeoffs in two Trichogramma species: influence of host size and Wollbachia infections affected by host availability. Ph.D. dissertation, University of California, Riverside.

Hohmann, C. L., R. F. Luck, and E. R. Oatman. 1988. A comparison of longevity and fecundity of adult Trichogramma platneri (Hymenoptera: Tichogrammatidae) reared from eggs of the cabbage looper and the Angoumois grain moth, with and without access to honey. J. Econ. Entomol. 1: 1307–1–312.

Housewart, W. R., D. T. Jennings, C. Welty, and S. G. Southard. 1983. Progeny production by Trichogramma minutum (Hymenoptera: Tichogrammatidae) utilizing eggs of Chortoneura fumiferana (Lepidoptera: Gelechiidae). Can. Entomol. 115: 1245–1252.

Huber, J. T. 1988. The species groups of Gonatocerus Nees in North America with a revision of the sulphuripes and ater groups (Hymenoptera: Mymaridae). Mem. Entomol. Soc. Can. 141: 1–109.

Jervis, M. A., and M.J.W. Copland. 1996. The life cycle, pp. 63–161. In M. Jervis and N. Kidd, [eds.], Insect natural enemies: practical approaches to their study and evaluation. Chapman & Hall, London, United Kingdom.

Jesu, R., and S. Laudonia. 1997. Gli stadi preimmaginali di Lathromeris cocidioyiiae Villagiani et Laudonia (Hymenoptera: Trichogrammatidae). Bol. Lab. Entomol. Agr. Filippo Silvestri 53: 13–17.

Kapila, R., and H. C. Agarwal. 1955. Biology of an egg parasite of Callosobruchus maculatus (Fab) (Coleoptera: Bruchidae). J. Stored Prod. Res. 31: 335–341.

Kruger, R., M. W. Johnson, R. L. Groves, and J. G. Morse. 2008. Host specificity of Anagrus epos: a potential biological control agent of Homalodisca vitripennis. Biocontrol 53: 439–449.

Lagace, M. 1998. Male fitness and optimal sex allocation in Trichogramma evanescens. M.S. thesis, McGill University, Montreal, QC, Canada.

Liu, S. S., G. M. Zhang, and F. Zhang. 1998. Factors influencing parasitism of Trichogramma dendrolimi on eggs of the Asian corn borer, Ostrinia furnacalis. Biocontrol 43: 273–287.

Logarzo, G. A., E. G. Virla, S. V. Triapitsyn, and W. A. Jones. 2004. Biology of Zagella delicata (Hymenoptera: Trichogrammatidae), an egg parasitoid of the sharpshooter
Tapajosa rubromarginata (Hemiptera: Clypeorrhyncha: Cicadellidae) in Argentina. Fla. Entomol. 87: 511–516.

Lund, H. O. 1938. Studies on longevity and productivity in Trichogramma evanescens. J. Agric. Res. 56: 421–439.

Mills, N. J., and U. Kuhlmann. 2000. The relationship between egg load and fecundity among Trichogramma parasitoids. Ecol. Entomol. 25: 315–324.

Morgan, D.J.W., S. V. Triapitsyn, R. A. Redak, L. G. Bezark, and M. S. Hoddle. 2000. Biological control of the glassy-winged sharpshooter: current status and potential future, pp. 167–171. In M. S. Hoddle [ed.], Proceedings, Califonia Conference on Biological Control, 11–12 July 2000, Riverside, CA. College of Natural and Agricultural Sciences, University of California, Riverside, CA.

Owen, A. K. 2005. Systematics of the Trichogrammatidae (Hymenoptera: Chalcidoidea): a molecular phylogeny of the family and worldwide revision of Ufens Girault. Ph.D. dissertation, University of California, Riverside.

Pak, G. A. 1986. Behavioural variations among strains of Trichogramma spp.: a review of the literature on host-age selection. J. Appl. Entomol. 101: 55–64.

Pavlik, J. 1993. The size of the female and quality assessment of mass-reared Trichogramma spp. Entomol. Exp. Appl. 66: 171–177.

Pinto, J. D. 2006. A review of the New World genera of Trichogrammatidae (Hymenoptera). J. Hymenopt. Res. 15: 38–163.

Pinto, J. D., and G. Viggiani. 2004. A review of the genera of Oligositini (Hymenoptera: Trichogrammatidae) with a preliminary hypothesis of phylogenetic relationships. J. Hymenopt. Res. 13: 269–294.

Pinto, J. D., S. I. Frommer, and S. A. Manweiler. 1987. The insects of jojoba, Simmondsia chinesis, in natural stands and plantations in southwestern North America. Southwest. Entomol. 12: 257–298.

Powers, N. R. 1973. The Biology and Host Plant Relations of Homalodisca incerta (Fowler) in Southern California. M.S. thesis, California State University, San Diego.

Purcell, J. H., S. R. Saunders, M. Hendson, M. E. Grebus, and M. J. Henry. 1999. Causal role of Xylella fastidiosa in oleander leaf scorch disease. Phytopathology 89: 53–58.

Ruberson, J. R., and T. J. Kring. 1993. Parasitism of developing eggs by Trichogramma pretiosum (Hymenoptera: Trichogrammatidae): host age preference and suitability. Biol. Control 3: 39–46.

SAS Institute. 1996. JMP IN, version 3. SAS Institute, Cary, NC.

Schmidt, J. M. 1994. Host recognition and acceptance by Trichogramma, pp. 165–200. In E. Wajnberg and S. A. Hassan [eds.], Biological control with egg parasitoids. CAB International, Wallingford, United Kingdom.

Takada, Y., S. Kawamura, and T. Tanaka. 2000. Biological characteristics: growth and development of the egg parasitoid Trichogramma dendrolimi (Hymenoptera: Trichogrammatidae) on the cabbage armyworm Mamestra brassicae (Lepidoptera: Noctuidae). Appl. Entomol. Zool. 35: 369–379.

Takiya, D. M., S. H. McMamey, and R. R. Cavichio. 2006. Validity of Homalodisca and of H. vitripennis as the name for glassy-winged sharpshooter (Hemiptera: Cicadellidae: Cicadellinae). Ann. Entomol. Soc. Am. 99: 648–655.

Taylor, T.H.C. 1937. The biological control of an insect in Fiji: an account of the coconut leaf-mining beetle and its parasite complex. Imperial Institute of Entomology, London, United Kingdom.

Thomson, P. H. 1982. Jojoba horticulture, pp. 57–162. In P. H. Thomson [ed.], Jojoba handbook, 3rd ed. Bonsall Publications, Bonsall, CA.

Tipping, C., S. V. Triapitsyn, and R. F. Mizell. 2005. A new host record for the egg parasitoid Paracentrobia americana (Girault) (Hymenoptera: Trichogrammatidae) of the proconiiine sharpshooter Homolodisca insolita (Walker) (Hemiptera: Cleyedorrhyncha: Cicadellidae). Fla. Entomol. 88: 217–218.

Triapitsyn, S. V. 2003. Taxonomic notes on the genera and species of Trichogrammatidae (Hymenoptera) — egg parasitoids of the Proconiiine sharpshooters (Hemiptera: Cleyedorrhyncha: Cicadellidae: Proconini) in southeastern USA. Trans. Am. Entomol. Soc. 129: 245–265.

Triapitsyn, S. V., and M.S. Hoddle. 2001. Search for and collect egg parasitoids of glassy-winged sharpshooter in southeastern USA and northeastern Mexico, pp. 133–134. In M. A. Tariq, S. Oswalt, and T. Esser [eds.], Symposium Proceedings, Pierce’s Disease Research Symposium, 5–7 December 2001, San Diego, CA. Copeland Printing, Sacramento, CA.

Triapitsyn, S. V., and M. S. Hoddle. 2002. Search for and collect egg parasitoids of glassy-winged sharpshooter in southeastern USA and northeastern Mexico, pp. 94–95. In M. A. Tariq, S. Oswalt, P. Blincoe, and T. Esser [eds.], Symposium Proceedings, Pierce’s Disease Research Symposium, 15–18 December 2002, San Diego, CA. Digital Logistix, Sacramento, CA.

Triapitsyn, S. V., L. G. Bezark, and D.J.W. Morgan. 2002. Redescription of Gonatocerus atricrusius Girault (Hymenoptera: Mymaridae), with notes on other egg parasitoids of sharpshooters (Hemiptera: Cicadellidae: Proconini) in northeastern Mexico. Pan-Pac. Entomol. 78: 34–42.

Triapitsyn, S. V., R. F. Mizell, III, J. J. Bossart, and C. E. Carlton. 1998. Egg parasitoids of Homalodisca coagulata (Hymenoptera: Cicadellidae). Fla. Entomol. 81: 241–243.

Turner, W. F., and H. N. Pollard. 1959. Life histories and behavior of five insect vectors of phony peach disease. U.S. Dep. Agric. Tech. Bull. 1189.

[UCOP] University of California, Office of the President. 2000. Report of the University of California Pierce’s disease research and emergency response task force. University of California, Oakland, CA.

Varela, L. G., R. J. Smith, and P. A. Phillips. 2001. Pierce’s Disease. University of California Agricultural and Natural Resources Publication 21600. University of California, Oakland, CA.

Virla, E. G. 1999. Aportes preliminares acerca de la bionoma de Paracentrobia subflava (Hym.: Trichogrammatidae), parasitode de Homopteros Cicadellideos Argentinos. Rev. Soc. Entomol. Argent. 58: 17–22.

Vungsilabutr, P. 1978. Biological and morphological studies of Paracentrobia andoi (Ishi) (Hymenoptera: Trichogrammatidae), a parasite of the green rice leafhopper, Nephotettix cincticeps Uhler (Homoptera: Deltocoephali dae). Esakia 11: 29–51.

Waage, J. K. 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation, pp. 63–95. In J. Waage and D. Greathead [eds.], Insect parasitoids. Academic, London, United Kingdom.

Waage, J. K., and N. S. Ming. 1984. The reproductive strategy of a parasitic wasp. I. Optimal progeny and sex allocation in Trichogramma evanescens. J. Anim. Ecol. 53: 401–415.

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