INTERSPECIFIC COMPETITION BETWEEN *GONATOCERUS ASHMEADI*, *G. TRIGUTTATUS,* AND *G. FASCIATUS* FOR GLASSY-WINGED SHARPSHOOTER EGG MASSES

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ABSTRACT

Interspecific competition between *G. ashmeadi*, *G. triguttatus* and *G. fasciatus* for GWSS egg masses was investigated in the laboratory using three experimental designs. Overall parasitism by *G. ashmeadi* was consistently higher (up to 76.0%) compared with *G. triguttatus* and *G. fasciatus*, for all three experimental designs. Exposing females to individual egg ages (1, 3 or 5 days) showed that *G. ashmeadi* parasitized a significantly higher (48.1%) proportion of GWSS eggs compared with *G. triguttatus*, whereas when females were exposed to all egg ages simultaneously, parasitism by *G. ashmeadi* and *G. triguttatus* was equivalent. Results from visual observations showed that *G. triguttatus* allocated a significantly higher (up to 36.4% and 22.9%, respectively) proportion of time to resting/grooming, compared with *G. ashmeadi* and *G. fasciatus*. *Gonatocerus fasciatus* spent a greater (19.6% and 9.6%, respectively) proportion of time off leaves with GWSS egg masses compared with *G. ashmeadi* and *G. triguttatus*. *Gonatocerus triguttatus* parasitized a significantly higher proportion (25%) of GWSS eggs compared with *G. fasciatus*, whereas time allocated to oviposition by each species was equivalent. *Gonatocerus ashmeadi* and *G. triguttatus* demonstrated aggressive behavior towards congeneric competitors for GWSS egg masses, whereas no aggressive behaviors were observed for *G. fasciatus*. The implications of these results for interspecific competition and biological control of GWSS by these three mymarid parasitoids are discussed.

INTRODUCTION

Gonatocerus ashmeadi has been resident in California since 1978 and genetic studies indicate it is native to the southeast U.S.A. and probably accompanied *H. coagulata* from its home range in the southeast U.S.A. *Gonatocerus triguttatus* has been imported from eastern Texas and released in California since 2001, while *G. fasciatus* was liberated in 2002 (CDFA, 2003). All three *Gonatocerus* species are mymarid parasitoids that attack GWSS eggs. The introduction of more than a single natural enemy to control a target pest as part of a classical biological control program may induce interspecific competition and result in either competitive exclusion or coexistence (Zwolfer, 1971; Myers et al., 1989). Coexistence of natural enemies can potentially lead to the disruption of biological control because interspecific competition can result in lower densities of the more efficient parasitoid which causes pest populations to be higher than what would occur with the more efficient species acting alone on the target population (Briggs, 1993; Rosenheim et al, 1995). A better understanding of the competitive interactions between *G. ashmeadi*, *G. triguttatus* and *G. fasciatus* for GWSS egg masses may provide insight into predicting and interpreting field outcomes following the establishment and proliferation of *G. triguttatus* and *G. fasciatus* in California, as they compete with the already well established and widely distributed *G. ashmeadi*. Irvin and Hoddle (2002) demonstrated that competition outcomes from laboratory studies can be contradictory and results greatly varied depending on the experimental designs used and the questions being addressed. Therefore, the following investigations were conducted to investigate which *Gonatocerus* parasitoid species is most competitive using three different experimental designs that varied GWSS egg age and egg density available for attack.

OBJECTIVES

Investigate interspecific competition between *G. ashmeadi, G. triguttatus* and *G. fasciatus* for GWSS egg masses of varying age and density.

RESULTS

Three experimental designs were used: the first involved exposing approximately 30 GWSS eggs of known age to one mated female *G. ashmeadi*, *G. triguttatus* and *G. fasciatus* (~24 hrs of age) for 24 hours in a 3 inch ventilated vial cage at 25^{o}C. This was repeated for eggs one, three and five days of age. The second experiment involved the above procedure, but exposed approximately 15 GWSS eggs of each age category (total of ~ 45 eggs), simultaneously to one mated female of each species. The third experiment involved exposing one egg mass (3-6 eggs and 24-48 hours of age) simultaneously to one mated female of each species searching together for one hour in a single 2 inch Petri-dish lined with moist filter paper. Visual observations for aggressive behavior were made every 5 minutes during the third experiment and behaviors at the observation point were recorded for each female. All experiments were replicated 20 times. The proportion of GWSS eggs parasitized by *G. ashmeadi*, *G. triguttatus* and *G. fasciatus* was calculated for each experiment and compared between species using Friedman's Chi-Square.

Overall parasitism by *G. ashmeadi* was consistently higher (up to 76.0%) compared with *G. triguttatus* and *G. fasciatus* for all three experimental designs (Figures 1-4). These results suggest that female *G. ashmeadi* may be more 'aggressive' than *G. triguttatus* and *G. fasciatus*, and therefore show greater potential as a biological control agent of GWSS. Results from laboratory studies presented here indicate that *G. ashmeadi* could out compete *G. triguttatus* and *G. fasciatus* in the field and hinder their successful establishment and impact in California. Previous studies have shown that *G. ashmeadi*, *G. triguttatus* and *G. fasciatus* demonstrate strong preferences for GWSS eggs aged two, three and four days, respectively (Irvin and Hoddle, in preparation), suggesting that field interspecific competition for egg masses may be less prevalent, compared with laboratory no choice situations when populations of GWSS of varying age are naturally co-occurring in field situations. Competitive advantages between parasitoid species are most likely to become important when host densities are low. It is possible that as GWSS biological control progresses in California, and GWSS populations diminish and egg masses become increasingly scarce, there may be a shift in parasitoid species dominance to the more competitively superior species at low egg mass densities.

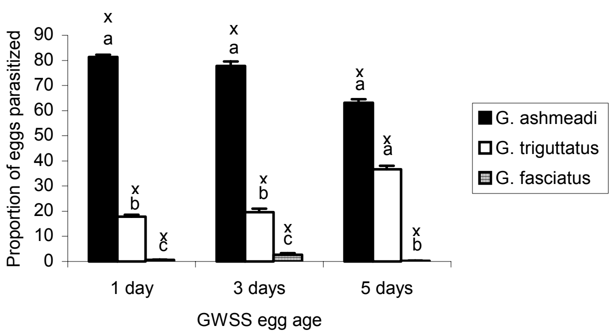

Figure 1. Proportion of GWSS eggs parasitized by *G. ashmeadi*, *G. triguttatus* and *G fasciatus* for eggs one, three and five days of age (different letters (x, y, z) indicate significant ($p < 0.05$) differences within species, different letters (a, b, c) indicate significant ($p < 0.05$) differences between species).

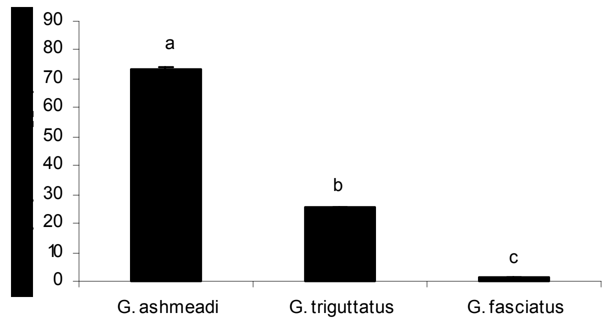

Figure 2. Over all proportion of GWSS eggs (combining one, three and five days of age) parasitized by *G. ashmeadi*, *G. triguttatus* and *G fasciatus* (different letters indicate significant ($p < 0.05$) differences between species).

When female *G. ashmeadi*, *G. triguttatus* and *G. fasciatus* were exposed to eggs one, three or five days of age concurrently in individual vials (experiment 1) the proportion of eggs parasitized by *G. triguttatus* increased from 17.8% for eggs one day of age, to 36.6% for eggs five days of age (Figure 1). This result was significant ($F = 3.14$, $df = 2$, $p = 0.053$) and supports previous research that showed under no choice conditions *G. triguttatus* demonstrated a preference for older hosts, by parasitizing a higher proportion of eggs three-six days of age (Irvin and Hoddle, in preparation). In the current study, parasitism by *G. ashmeadi* was 63.6% and 58.2% higher than *G. triguttatus*, when females were exposed to eggs one and three days of age, respectively. Whereas for eggs five days of age, there was no significant difference in parasitism between these two species. This indicates that *G. triguttatus* larvae, resulting from eggs deposited in GWSS eggs five days of age, were more able to compete with *G. ashmeadi* larvae because this more preferred GWSS egg age may have provided a highly favorable environment for *G. triguttatus* development. Alternatively, *G. triguttatus* females aggressively defended eggs from *G. ashmeadi* and prevented multiparasitism from occurring. In contrast, the proportion of eggs parasitized did not significantly vary between egg ages for *G. ashmeadi* ($F = 2.62$, $df = 2$, $p = 0.08$) and *G. fasciatus* ($\chi^2 = 1.93$, $df = 2$, $p = 0.38$) (Figure 1), whereas previous studies have shown that *G. ashmeadi* and *G. fasciatus* demonstrate strong preferences for eggs one and three days of age, respectively (Irvin and Hoddle, in preparation). Parasitism by *G. fasciatus* may not have been significant between egg ages in the current study, because interspecific competition and potential mutual interference caused extremely low parasitism rates (0.3-2.7%) (Figure 1). *Gonatocerus ashmeadi* may not have demonstrated a preference for GWSS eggs three days of age in the current study because exposure time was higher for the current study (24 hours compared with 2 hours in the previous study), perhaps causing higher rates of parasitism at less preferred egg ages, or the presence of competitors in the current study may have initiated *G. ashmeadi* aggressiveness and oviposition.

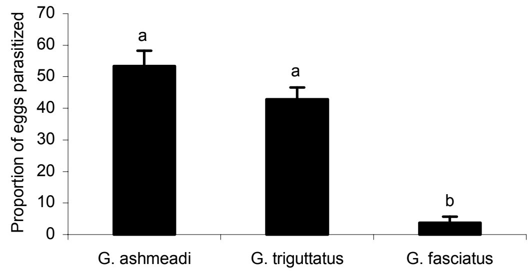

Figure 3. Percentage of GWSS eggs parasitized by *G. ashmeadi*, *G. triguttatus,*and *G fasciatus* when eggs one three and five days of age are presented simultaneously to one female of each species (see Figure 2).

Irvin and Hoddle (2002) showed that competition outcomes between *G. ashmeadi* and *G. triguttatus* varied greatly depending on the experimental design and GWSS egg density used. In the current research, pooling results from exposing females to individual egg ages showed that *G. ashmeadi* parasitized a significantly higher (48.1%) proportion of GWSS eggs compared with *G. triguttatus* (Figure 2), whereas when females were exposed to all egg ages simultaneously, parasitism by *G. ashmeadi* and *G. triguttatus* was equivalent (Figure 3). This may be due to *G. ashmeadi* out competing *G. triguttatus* when females were only provided eggs one or three days of age, since these ages are more favorable for *G. ashmeadi* development, and *G. triguttatus* prefers older hosts (Irvin and Hoddle, in preparation). We speculate that when *G. ashmeadi* and *G. triguttatus* were exposed simultaneously to eggs one, three and five days of age, females parasitized egg ages most preferred by each species, thereby decreasing interspecific competition and resulting in equivalent parasitism rates between species. These results may have important implications for the field environment, where a range of host ages are present at one time, and may suggest that *G. ashmeadi* and *G. triguttatus* can coexist in California without significant interference.

Parasitism by *G. fasciatus* was consistently significantly lower (17.4-76.0% lower) than both *G. ashmeadi* and *G. triguttatus* for all three experimental studies (Figures 1-4). *Gonatocerus fasciatus* may have performed poorly because exposure to GWSS eggs was restricted to one or 24 hours in these studies, and *G. fasciatus* being smaller may require a longer period of time for each individual host handling, and lay fewer eggs at each oviposition event compared with *G. ashmeadi* and *G. triguttatus*. Lifetime fecundity, longevity or offspring production was not investigated in the current studies so it is unknown whether *G. fasciatus* may perform more effectively in the field, over many generations. However, female *G. fasciatus* are capable of producing two or more offspring per *H. coagulata* egg and gregarious reproduction may be advantageous early in the spring when GWSS egg masses are relatively rare and parasitism levels are low (Triapitsyn et al., 2003).

There are many factors that influence the competitive ability of female Hymenoptera. Extrinsic competition refers to the exploitation of the host population (Zwolfer, 1971) and involves factors associated with host finding efficiency, host discrimination between parasitized and unparasitized hosts, aggressive behavior between adult parasitoids, reproductive capacity of female parasitoids, host developmental stage attacked, sex ratio, and phenological synchronization with the host (Lewis et al., 1990; Tumlinson et al., 1993). When multiparasitism does occur, intrinsic competition refers to the interaction between immature parasitoids and involves larval combat or physiological suppression (Chow and Mackauer, 1984; Lawrence, 1988; DeMoraes et al., 1999). The competitive inferiority of *G. fasciatus* shown in these studies may be attributed to poor competitive ability of *G. fasciatus* larvae. Firstly, eggs oviposited by female *G. fasciatus* are conceivably smaller than *G. ashmeadi* and *G. triguttatus*, due to comparative differences in female size between species (Triapitsyn et al., 2003) . Larvae that emerge from larger eggs may potentially give rise to larger parasitoid larvae, which may tend to be better competitors, especially if they hatch earlier (Collier and Hunter, 2001). Secondly, *G. fasciatus* larvae probably do not participate in larval combat, since gregarious larvae often frequently contact one another under normal development (Salt, 1961), and therefore such species may be at an intrinsic disadvantage against congeneric species cohabiting a resource.

Alternatively, the competitive inferiority of *G. fasciatus* may simply be due to subordinate aggressiveness when competing for egg masses with congenerics. For example, in one hour egg age choice experiments where oviposition was required, Irvin and Hoddle (in preparation) showed that 115% and 65% additional female *G. fasciatus* were required to obtain sufficient replication when compared with *G. ashmeadi* and *G. triguttatus*, respectively. Results from the observation study (experiment 3) presented here showed that *G. fasciatus* allocated a significantly higher proportion (31.5%) of time to resting/grooming, compared with oviposition, whereas female *G. ashmeadi* allocated equal time to both activities (Figure 5). Results from both studies may suggest that female *G. fasciatus* are less aggressive than *G. ashmeadi* and *G. triguttatus*, or under the experimental conditions used oviposition motivation was diminished. Furthermore, 39.6% of time allocated by female *G. fasciatus* was spent off leaves with GWSS egg masses (Figure 5), and it was observed that *G. ashmeadi* and *G. triguttatus* often aggressively protected the GWSS egg mass, sometimes excluding access by *G. fasciatus*. Also, female *G. fasciatus* are smaller than *G. ashmeadi* and *G. triguttatus* (Triapitsyn et al., 2003). Together these observations may explain why *G. fasciatus* spent significantly (9.6-19.6%) more time off the egg mass compared with both *G. ashmeadi* and *G. triguttatus* (Figure 5).

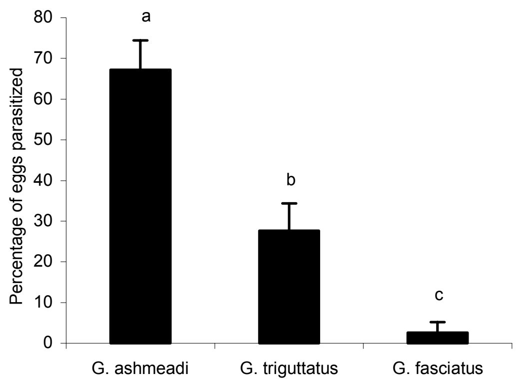

Figure 4. Percentage of eggs parasitized by *G. ashmeadi*, *G. triguttatus* and *G fasciatus* when one GWSS egg mass is presented simultaneously to one female of each species (See Figure 2).

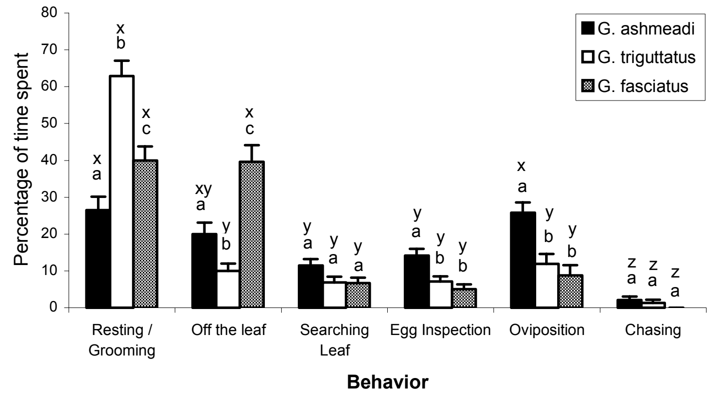

Figure 5. Proportion of time spent in each quantified behavior for female *G. ashmeadi*, *G. triguttatus* and *G fasciatus*, when one GWSS egg mass is presented simultaneously to one female of each species (See Figure 1)

In the Petri-dish observation trial (experiment 3), parasitism by *G. triguttatus* was significantly (39.6%) lower compared with *G. ashmeadi* (Figure 4). This contradicts a similar study that showed that parasitism by *G. triguttatus* was 53% higher compared to *G. ashmeadi* (Irvin and Hoddle, 2002) and iterates the question raised by Irvin and Hoddle (2002), of which experimental designs should be used to decide which parasitoid species shows the most potential as a classical biological control agent for GWSS. *Gonatocerus triguttatus* may have performed differently in the current study because an additional species (*G. fasciatus*) was incorporated into the design. Data from the current study showed that 62.9% of behavioral observations for *G. triguttatus* were resting/grooming, which was significantly higher (36.4% and 58.9%, respectively), when compared with *G. ashmeadi* and *G. fasciatus* (Figure 5). This suggests that female *G. triguttatus* may have a longer pre-oviposition period and require more time resting before ovipositing, or that when three parasitoid species are present concurrently, the assertiveness of female *G. triguttatus* declines.

In Experiment 3 (visual observations in Peri dishes), *G. triguttatus* parasitized a significantly higher proportion (25%) of GWSS eggs compared with *G. fasciatus* (Figure4), whereas time allocated to oviposition by each species was equivalent (Figure 5). This may indicate that *G. triguttatus* is more competitive when ovipositing or its larvae are more aggressive towards congeneric species. Scanning electron microscopy of *G. triguttatus* larvae four days of age has revealed that *G. triguttatus* larvae possess anterior tusk-like appendages, that could possibly be used in larval combat for host procurement (Irvin and Hoddle, in preparation). Irvin and Hoddle (in preparation) conducted a study that involved exposing one GWSS egg mass to one female *G. triguttatus* for one hour, and one hour following the removal of *G. triguttatus*, the same egg mass was exposed to one female *G. ashmeadi* for one hour. Parasitoid emergence data from egg masses in which ovipositor insertion of both species was observed were analyzed. Results showed that the proportion of *G. triguttatus* offspring emergence was 88%, compared with 12% for *G. ashmeadi* when *G. triguttatus* oviposited first (Irvin andHoddle, in preparation). However, when the sequence of species introduction was reversed, the proportion of *G. ashmeadi* emergence was 49%, compared with 51% for *G. triguttatus*. With a four-hour intermission between introducing *G. triguttatus* to the previously parasitized egg mass the proportion of *G. ashmeadi* offspring were not significantly higher than *G. triguttatus*. Only with a 24-hour intermission between female introductions, did *G. ashmeadi* produce significantly more offspring (64%) than *G. triguttatus* (36%) (Irvin and Hoddle, in preparation). These results support the theory that *G. triguttatus* larvae may be superior competitors when multiparasitism of GWSS egg masses occurs.

Zwolfer (1971) proposed that due to life history trade-offs, parasitoid species that are intrinsically inferior should win in extrinsic competition, and vice versa. Therefore it is possible, that while *G. fasciatus* performed poorly in the current studies, females may be extrinsically superior in the field due to potentially higher reproduction rates (gregarious reproduction), oviposition preference for young GWSS egg masses, and greater host finding efficiency at low host densities. A previous study investigating percentage parasitism and offspring emergence of each species showed that parasitism by *G. fasciatus* was up to 15.9% lower than *G. ashmeadi* and *G. triguttatus*. But because of the gregarious reproduction habit, *G. fasciatus* offspring emergence was 77.2% and 82.9% higher compared with *G. ashmeadi* and *G. triguttatus*, respectively (Irvin and Hoddle, in preparation).

CONCLUSIONS

- Overall parasitism by *G. ashmeadi* was consistently higher (up to 76.0%) compared with *G. triguttatus* and *G. fasciatus* for all three experimental designs suggesting that *G. ashmeadi* may show greater potential as a biological control agent of GWSS and could out compete *G. triguttatus* and *G. fasciatus* in the field.
- The aggressive behavior demonstrated by *G. ashmeadi* and *G. triguttatus*, towards other females, may give these species a competitive advantage over *G. fasciatus* which does not display similar aggressive tendencies.
- Parasitism by *G. fasciatus* was consistently significantly lower (17.4-76.0%) than both *G. ashmeadi* and *G. triguttatus* for all three experimental studies, suggesting that this species may be an inferior competitor under laboratory conditions. However *G. fasciatus* may be superior in the field, due to potentially higher reproduction rates, younger host age attacked and greater host finding efficiency.

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