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INTRASPECIFIC COMPETITION FOR RESOURCES BY *ORMIA DEPLETA* (DIPTERA: TACHINIDAE) LARVAE

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ABSTRACT

Ormia depleta is a parasitoid of pest mole crickets in the southeastern United States. From 2 to 8 larvae of *O. depleta* were placed on each of 368 mole cricket hosts and allowed to develop. The weights of the host crickets, number of larvae placed, number of resulting pupae, and the weights of those pupae were all factored to determine optimal parasitoid density per host under laboratory rearing conditions. Based on larval survival and pupal weight, this study indicates that 4-5 larvae per host is optimal for laboratory rearing.

Key Words: biocontrol, *Scapteriscus*, parasitoid, superparasitism

RESUMEN

Ormia depleta es un parasitoide de grillotopos en el sureste de los Estados Unidos. Entre 2 y 8 larvas de *O. depleta* se colocaron en 368 grillotopos huéspedes y se dejaron madurar. El peso de los huéspedes, el número de larvas de *O. depleta* colocadas, el número de pupas resultantes y el peso de las pupas fueron usados para determinar la densidad optima de parasitoides en cada huésped para ser usadas en la reproducción de este parasitoide en el laboratorio. Nuestros resultados muestran que entre 4 y 5 larvas por cada grillotopo es la densidad optima para la reproducción en el laboratorio de este parasitoide.

Translation provided by the author.

Ormia depleta (Wiedemann) is a parasitoid of *Scapteriscus* spp. mole crickets, imported pests of turf and pasture grasses in the southeastern United States (Frank et al. 1998). Female flies are phonotactic to the call of the male *Scapteriscus* spp. crickets (Fowler 1987; Fowler & Garcia 1987; Walker et al. 1996). *Ormia depleta* was originally collected from Piracicaba, Brazil, for use as a biocontrol agent against *Scapteriscus* spp. mole crickets and was first released in 1988 (Frank et al. 1996). Since then, it has established in at least 38 counties in Florida, and in some it has suppressed mole cricket populations (Parkman et al. 1996).

Ormia depleta can be a difficult organism to maintain in a laboratory colony. One of the factors that makes it difficult to rear lies in the variable and generally low proportion of gravid females obtained under the current laboratory rearing protocol. For example, a colony of 100 individuals may in 1 generation produce 20 gravid females and in the next only 1 or 2 or even zero (R. Hemenway, Dept. Entomology and Nematology, University of Florida, personal communication). Therefore, it is necessary to determine the best way to use the number of planidia available in any 1 generation to produce the maximum number of healthy pupae to start the next generation. This must also be balanced with the expense of rearing the mole cricket hosts, which are very labor intensive to maintain. Current laboratory protocol requires hand inoculation of 3 planidia under the posterior margin of the pronotum of each host (R. Hemenway, Dept. Entomology and Nematology, University of Florida, personal communication). Fewer planidia per host may increase the chances of survival by reducing competition and subsequently producing larger pupae. This would, however, require more hosts to produce enough pupae to maintain the colony. Inoculating hosts with more planidia may increase the number of pupae and reduce the cost associated with host rearing, but superparasitism should be avoided to minimize consequences associated with production of pupae and adults with reduced fitness.

Previous research with *O. depleta* showed that there was no relationship between the number of planidia used to inoculate the host and the number of pupae produced (Fowler 1988), but my preliminary research suggested that higher numbers of pupae could be produced than previously recorded. Additionally, Fowler & Martini (1993) found a weak correlation between host size and the weights of the flies produced. In the present experiment, the host-parasitoid relationship was also examined to determine (1) whether host weight should be a selecting factor and (2) to determine whether an increase in the number of pupae produced per host could be achieved without sacrificing the survivability or vigor of the larvae due to superparasitism. In addition to varying the

number of planidia applied to each host, the weights of the host mole crickets were measured during inoculation to see whether larger hosts could provision more parasitoids. These factors were examined to determine their effect on the number of pupae produced, the mean weight of those pupae, and the survivability of the larvae to the pupal stage.

Materials and Methods

During the maintenance of the laboratory colony of *O. depleta*, *S. abbreviatus* Scudder from the University of Florida mole cricket rearing lab were individually weighed and inoculated with varying numbers of *O. depleta* planidia. The weights of the hosts ranged from 0.54-1.59 g and the weights of the hosts were not considered in determining the number of planidia used to inoculate each individual. The number of planidia per host ranged from 2-8, with most of the mole crickets being inoculated with 3, 4, or 5 planidia. These numbers were favored because they are the numbers most frequently used in the routine maintenance of the colony. Host crickets were randomly assigned to particular numbers of planidia. The numbers of mole crickets inoculated with 2, 3, 4, 5, 6, 7, and 8 planidia were 12, 108, 110, 52, 43, 32, and 11, respectively. Each mole cricket was then returned to an individual 20-dram (90-mL) plastic vial filled with moist sand, and the larvae were allowed to develop for 12 d at a room temperature of ~26°C. At that time, the pupae were collected and weighed. Statistical analysis was performed with the general linear model procedure (SAS Institute 2001). Regression analysis was used to determine the effect of the number of planidia on pupal production, the mean pupal weight, and the survivability. Additionally, the weights of the host mole crickets were analyzed to determine their effect on the survivability of the planidia used. Where applicable, the differences between the means were determined by Duncan's multiple range test (SAS Institute 2001). Regression analyses were conducted to determine the relationships between each of these factors (SAS Institute 2001).

To determine the effect that host mole cricket weight had on planidia survival, the number of pupae produced and the mean weights of those pupae and mole cricket weights were rounded to the nearest 0.1 g to place them into weight classes. Additionally, weight classes which had only 2 or fewer samples were eliminated. In this case, the smallest weight class, 0.70 g (n = 2) and the 2 largest weight classes, 1.5 g (n = 2) and 1.6 g (n = 2) were eliminated from the statistical analysis. The survival of the planidia on hosts in the remaining weight classes were analyzed by ANOVA PROC GLM (SAS Institute 2001).

Results

The mean number of pupae produced relative to the number of planidia used is shown in Fig. 1. There is an increase in the number of pupae produced as the number of planidia increases (F = 15.77; df = 360; $P < 0.0001$) and significant differences between the means of the treatments. The regression analysis (Fig. 2) supports this trend and indicates an increase of 0.41 pupae for each increase in planidia (F = 83.77; $P < 0.0001$; r^2 = 0.19).

Fig. 3 shows the survival of planidia grouped by the number of planidia placed on each host. ANOVA is significant for the model (F = 2.57; df = 360; $P < 0.02$). Fig. 4 is the regression analysis of the same data set (F = 9.16; $P < 0.002$; r^2 = 0.03), indicating an approximate 3% reduction in survival for each increase in the level of planidia density.

The analysis of the number of planidia used as it affected the mean weight of the pupae produced was found to be significant at the 0.10 level, but not at the 0.05 level by ANOVA (F = 2.06; df = 360; P = 0.06). There was some significance among the means as indicated by the letters over the bars in Fig. 5. The regression analysis for the mean weights of pupae produced as a function of number of planidia inoculated per host is in Fig. 6 (F = 8.33; $P < 0.004$; r^2 = 0.02) and indicates a reduction in the mean weight of the pupae of 2.2 mg for each additional planidium.

The effect that host mole cricket weight had on the number of pupae produced was not significant when analyzed by ANOVA (F = 1.06; df = 361; P = 0.39). The effect of host mole cricket weight on the survivability of the larvae was significant (F = 2.12; df = 361; P = 0.05). The effect of host mole cricket weight on mean weight of the pupae produced was highly significant (F = 3.49; df = 361; $P < 0.002$) (Fig. 7). The regression analysis can be seen in Fig. 8 (F = 20.62; $P < 0.0001$; R^2 = 0.05).

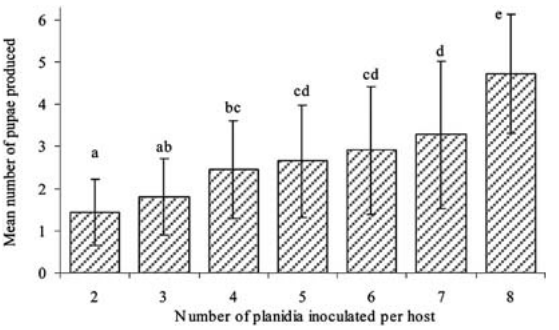

Fig. 1. The effect of planidia density used to inoculate mole crickets on the number of pupae produced (error bars indicate standard deviation, significantly different means indicated by letters over bars as determined by Duncan's procedure, α = 0.05).

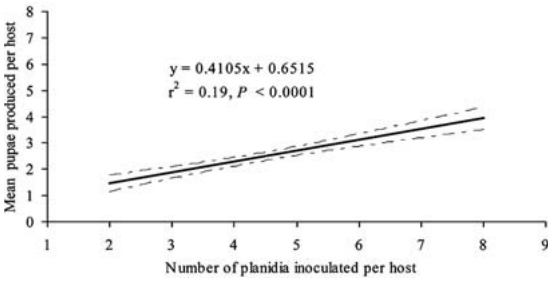

Fig. 2. The effect of number of planidia used to inoculate mole crickets on the number of pupae produced; regression analysis with 95% confidence intervals.

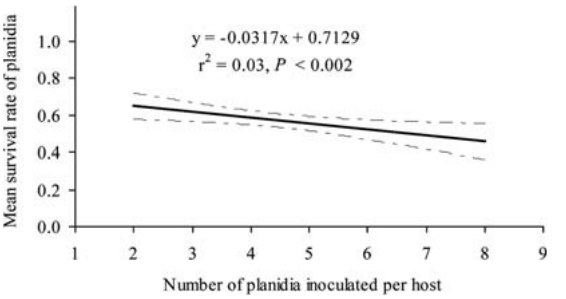

Fig. 4. The effect of number of planidia used to inoculate mole crickets on the survival rate of the larvae to the pupal stage; regression analysis with 95% confidence intervals.

DISCUSSION

The number of planidia used to inoculate host mole crickets as well as the weight of those mole crickets are important factors to the rearing of *O. depleta* in the laboratory. Although these data do not clearly dictate a specific protocol that should be used, they do provide a framework that would allow anyone rearing *O. depleta* to structure an inoculation protocol specific to their needs. When large numbers of planidia are available with only a few possible hosts, the data suggest that inoculating mole crickets with more planidia would increase the production of pupae. Too many, however, would result in reduced pupal size. At times when fewer planidia are available and maximum survivability is required, inoculating 2 or 3 planidia per host would be more effective. Alternatively, if larger pupae are desired, reducing the number of planidia per host along with using larger hosts would achieve the desired goal. Therefore, the current method of inoculating 3 planidia per host is less efficient than inoculating 4 or 5, because there is no significant reduction in pupal size, but there is a significant increase in the number of pupae produced. The reduction in size that results from the use of 8 planidia, or possibly more, would likely be detrimental to the colony of flies. Furthermore, these data only show a reduction in larval survival, they do not indicate other negative factors that may be associated with reduced size. Future research may be needed to determine whether individuals developing from heavily parasitized hosts show any reduction in longevity, ability to mate, or in fecundity as well as how the reduction in size of a generation may affect the size or fitness of future generations of flies.

Due to the flies' phonotactic search method for hosts and the solitary nature of the adult mole crickets, it would seem advantageous for the flies to maximize the number of offspring per host. Under field conditions, however, the mean number of *O. depleta* larvae found within trapped *Scapteriscus* hosts is less than 2 (Amoroso 1990).

The closely related *O. ochracea* Bigot, a parasitoid of *Gryllus* spp. crickets, has an optimal laboratory clutch size of 4-5 larvae per host, but under field conditions only deposit 1.7 ± 1.0 (SD). larvae (Adamo et al. 1995). There must be some ecological advantage to depositing fewer larvae than what would appear to be the optimal number.

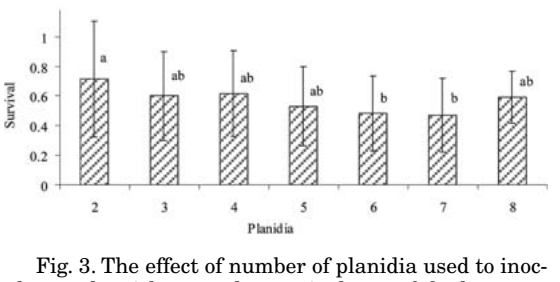

Fig. 3. The effect of number of planidia used to inoculate mole crickets on the survival rate of the larvae to the pupal stage (error bars indicate standard deviation; significantly different means indicated by letters over bars as determined by Duncan's procedure, $\alpha = 0.05$).

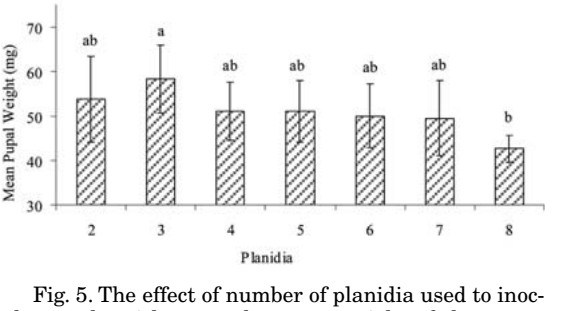

Fig. 5. The effect of number of planidia used to inoculate mole crickets on the mean weight of the pupae produced (error bars indicate standard deviation; significantly different means indicated by letters over bars as determined by Duncan's procedure, $\alpha = 0.05$)

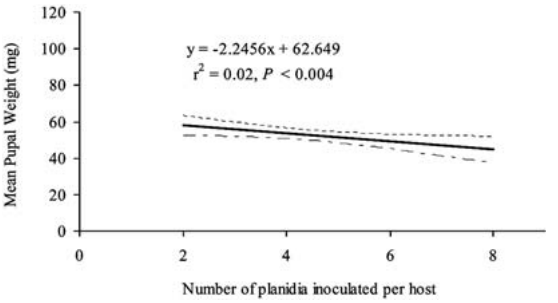

Fig. 6. The effect of number of planidia used to inoculate mole crickets on the mean weight of the pupae produced; regression analysis with 95% confidence intervals.

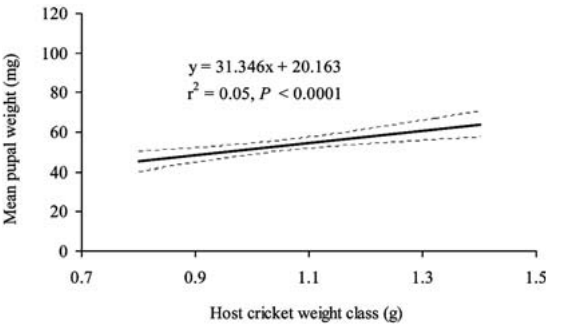

Fig. 8. The effect of host cricket weight class on the mean weight of the pupae produced; regression analysis with 95% confidence intervals.

It may be that *O. depleta* does not suffer from any shortage of hosts. Mole crickets are certainly abundant and calling during certain times of the year, but at other times seemingly unavailable. *Ormia depleta* may be able to find non-calling mole crickets in other ways, or there may be alternative hosts. Adamo et al. (1995) concluded that host availability was not a likely factor in determining the number of larvae deposited on hosts by *O. ochracea*. Another possibility is that *O. depleta* is responding to a factor in the field that is greatly reduced in the laboratory, such as mortality of the hosts. Under laboratory conditions, mole crickets suffer little disease and no predation. Higher host mortality in the field may make it advantageous for parasitoid offspring to be located in multiple hosts and subsequently reduce the effects on their population due to host predation. This hypothesis is somewhat strengthened by the fact that *O. depleta* does not deposit eggs, but planidia larvae, so the female's investment in parasitizing a host is already greater than that of an egg layer. Another laboratory factor that should be considered is hand-inoculating. The mole crickets that are hand-inoculated are unable to protect themselves in any way and have no opportunity to use any natural defenses such as brushing of planidia or retreating underground.

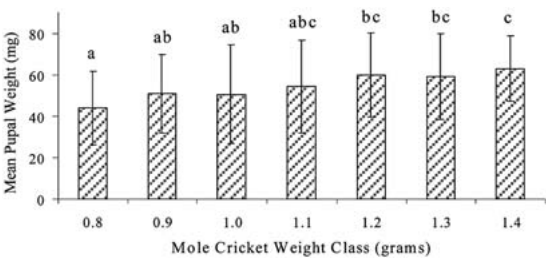

Fig. 7. The effect of host cricket weight on mean pupal weight (error bars indicate standard deviation; significantly different means indicated by letters over bars as determined by Duncan's procedure, $\alpha = 0.05$).

This type of grooming has been observed in *Gryllus* spp. crickets after an encounter with *O. ochracea* (Adamo et al. 1995).

The final reason for the low numbers of larvae found in field-captured hosts may be that there is a reduction in fitness caused by the high numbers of larvae used in this experiment. Reduced size is the easiest type of fitness reduction to observe, but many others may be at work. It may be that, due to competition, certain key resources are not available in sufficient amounts for the flies reared under superparasitoid conditions for the resulting adult flies to develop, mate, locate hosts, or reproduce properly. Many physiological deficiencies may result from superparasitoidism, and they may not be obvious either externally, or immediately (Waage & Ng 1984). These possibilities still remain for future research.

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