Selected Factors Influencing the Number of Eggs Laid During Each Ovipositional Attack by *Meteorus leviventris* (Hymenoptera:Braconidae)

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Introduction

Meteorus leviventris (Wesmael) is a gregarious, internal parasitoid of the black cutworm, *Agrotis ipsilon* Hufnagel. The parasitoid attacks the larval stage of the black cutworm, depositing during each attack a group of eggs defined as a clutch, and numbering between 1 and 48 eggs (Grafton-Cardwell, unpublished data). The number of progeny emerging from field collected cutworms has been found to average 27 (El-Minshawy 1971; Schoenbohm 1975).

Gregarious parasitoids, such as *M. leviventris*, deposit a variable number of eggs per ovipositional attack (Benson 1973). Therefore, it becomes necessary to continuously observe a parasitoid in order to accurately quantify the number of ovipositional attacks it has made on a host (van Lenteren et al. 1978).

The ability to predict average clutch size under specific conditions can provide a tool for estimating the number of ovipositional attacks made on a host when parasitoids cannot be observed. Therefore, determinations of the relationships between specific factors and clutch size laid by *M. leviventris* were made. The research was supported by EPA Grant #R805429-01-0.

Materials and Methods

The five factors chosen for this study were: 1) time of day, 2) parasitoid age, 3) intrinsic differences between parasitoids, 4) duration of ovipositional attack, and 5) host availability. Two experiments were conducted in order to examine the effects of these two factors on clutch size.

Adult females of *Meteorus leviventris* were selected for use in the experiments from a laboratory colony maintained on *Agrotis ipsilon.* All parasitoids used had emerged within 6 hours of the experiments and were provided a 50% honey-water solution as a food source throughout the experiments. Black cutworm larvae were selected from a colony maintained on an artificial diet as modified by Reese et al. (1972). Host size was standardized at 40-60 mg. for all experiments. Hosts parasitized in the experiments were placed individually on diet, allowed to mature for 4 days in an environmental chamber (26° C, 12L:12D), and then dissected. At this temperature, the parasitoid eggs began hatching on the 4th day. Both mature eggs and 1st instars were found in dissected hosts. Hosts were not dissected earlier because the less mature eggs were difficult to locate and remove.

Analyses of time of day and parasitoid age were performed using three different host densities (4, 8, and 12 hosts/12 hrs). The host densities were selected to be equal to or in excess of the average number of hosts attacked per 12 hours by *M. leviventris*. This experiment was conducted in a growth chamber (26° C, 12L:12D). Nine adult female parasitoids were placed in individual oviposition cages, as described by Schoenbohm (1975), at the start of the dark cycle. Three groups of three cages were utilized in which the cages in each group contained 4, 8, and 12 nonparasitized hosts, respectively. Every 12 hours, exposed hosts were replaced by an equal number of nonparasitized hosts. This was repeated until the parasitoid died. The number of parasitoid progeny per host was determined by dissection.

The remaining factors were examined in daylight (12L:12D) at room temperature (25° C). Ten 4-day-old female parasitoids were placed in individual oviposition cages and to each of which a nonparasitized host was exposed. If the parasitoid did not accept the host for oviposition within five minutes, the host was removed. If the host was accepted, the duration of ovipositional attack was recorded, and after dissection the number of progeny per host was determined. This procedure was repeated several times a day over a 12-day period for each parasitoid.

Results

Time of Day

When *M. leviventris* females were continuously supplied with hosts, they laid significantly more total eggs during the dark 12-hour period ($p = .05$) than during the light 12-hour period each day (Fig. 1). Oviposition between host densities was not found to be significantly different ($p = .05$). Since feeding and egg maturation may be affected by a diurnal rhythm (Engelmann 1970), it was thought that this rhythm might influence clutch size. However, the number of eggs laid per host (Fig. 2) was not found to be significantly different ($p = .05$) for the two periods. Time of day was found to have a significant effect on the total number of eggs laid, but did not have a significant effect on the number of eggs laid per host.

Parasitoid Age

When hosts were provided in numbers equal to or in excess of what is usually parasitized by *M. leviventris* (an average of 4 hosts/12 hrs), clutch size (y) was found to decrease with increasing parasitoid age (x) after peak oviposition according to the decay curve $y = 21.54e^{-.ix}$ ($r^2 = .59$) (Fig. 3). Clutch size decreased from 26 progeny to 3 progeny per host. An analysis of variance performed on the data indicated that the age of the parasitoid had a significant effect ($p = .05$) on clutch size.

Intrinsic Differences between Parasitoids

When parasitoids received fewer hosts than they can easily attack, all were observed to respond to the first host placed near them within five minutes. Each parasitoid was exposed to the same number of hosts, but each showed a different level of acceptance of hosts. Seven

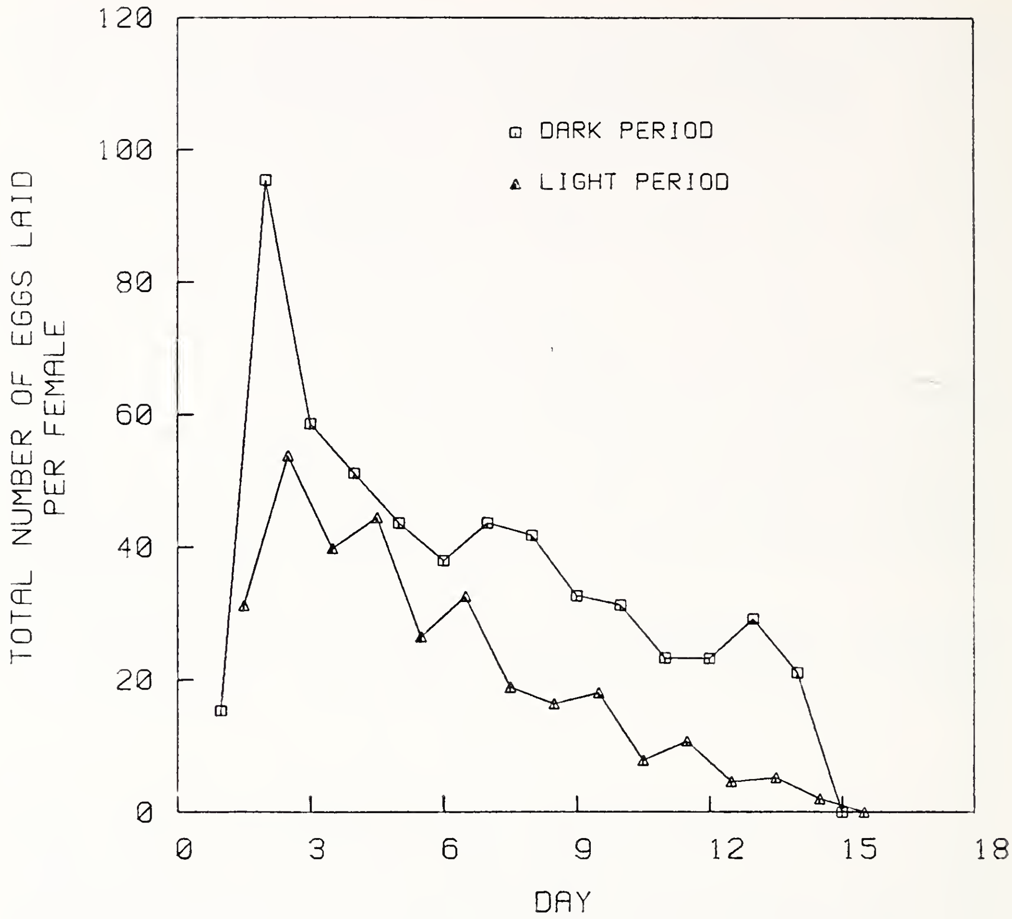

FIGURE 1. *Average daily egg deposition by* M. leviventris *divided into dark and light periods.*

of the parasitoids attacked 6 or 7 hosts out of 20 exposures to hosts. The other parasitoids attacked only 3 hosts each. It was found that clutch size was significantly different (p = .05) between the 7 parasitoids which attacked similar numbers of hosts (Table 1). Average clutch size for these parasitoids ranged from 19.6 to 29.4 eggs per host. Parasitoids which experienced the same experimental conditions laid significantly different clutch sizes.

Duration of Ovipositional Attack

Meteorus leviventris typically inserts its ovipositor into the host for an average time span of 1 second, but has been observed to leave it inserted for up to 3 minutes (Schoenbohm 1975). Three periods of ovipositional duration (1 sec; 2-5 sec; 6+ sec) were compared with the number of eggs laid during the corresponding ovipositional attack. The duration of ovipositional attack was not found to have a significant effect (p = .05) on clutch size (Table 1).

Host Availability

When parasitoids were provided hosts in numbers lower than they can easily attack (less than 4 hosts/12 hrs), clutch size per host

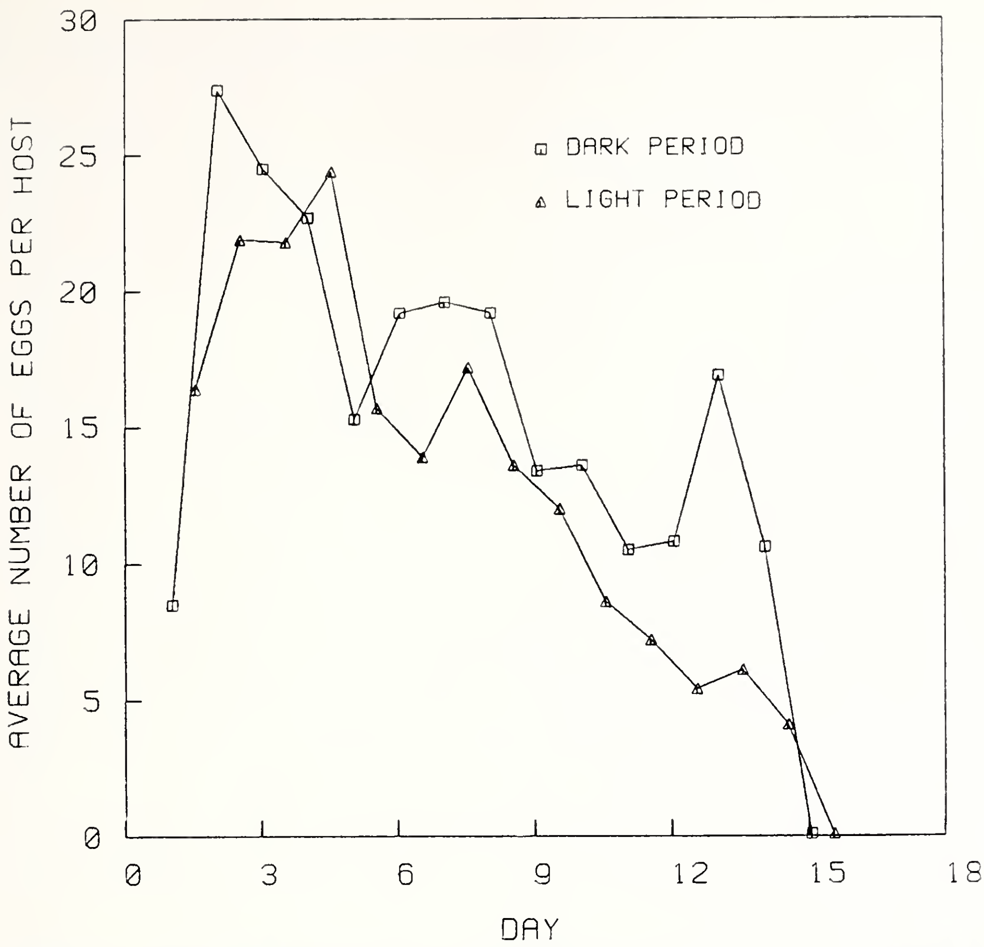

FIGURE 2. *Average daily number of eggs laid by* M. leviventris *per host divided into dark and light periods.*

TABLE 1. *Summary of the Analysis of Variance for the effects of duration of ovipositional attack (L) and intrinsic differences between parasitoids (P) on clutch size.*

Source	Degrees Freedom	F test
Duration of attack (L)	2	.6
Parasitoids (P)	6	9.95**
Error	44	

** Significant at the $p = .01$ level.

remained high throughout the parasitoid's life (Fig. 4). Clutch size (y) decreased from 30 to 20 progeny per host with increasing parasitoid age (x), and was found to be described by the equation $y = 29.74e^{-.02x}$ ($r^2 = .55$) for the conditions of this experiment. The rate of change was small and the intercept high when parasitoids were provided few hosts (Fig. 4). Clutch size during a single oviposition attack did not exceed 48 eggs, which was within the range of progeny the host can support (Grafton-Cardwell, unpublished data).

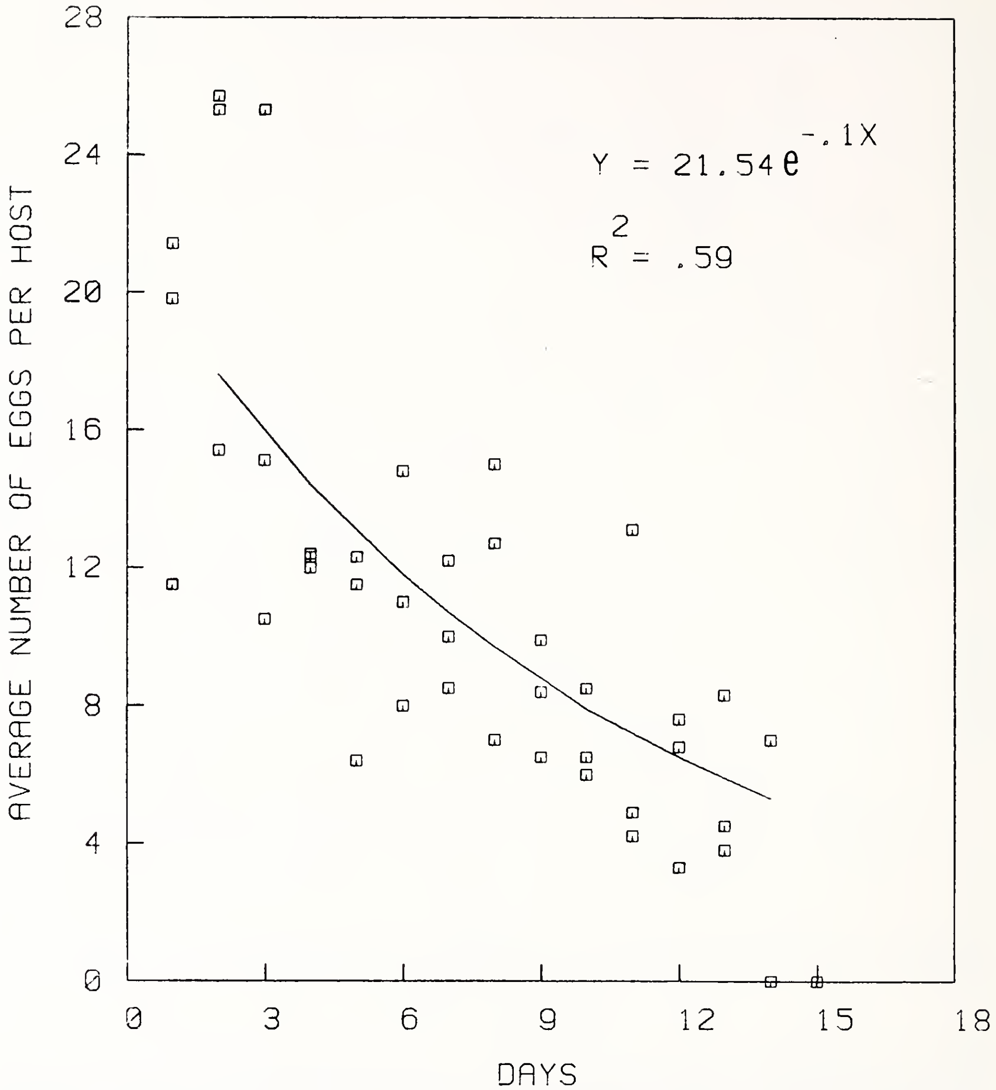

FIGURE 3. *Effect of* M. leviventris *age on clutch size during continuous host supply.*

Discussion

Host size is a factor known to influence the number of eggs laid by a parasitoid with each attack on a host (Salt 1934). This factor was standardized in all experiments to remove its effect, but should be considered in future experiments with *M. leviventris.*

Of the five factors which were examined, three were found to have a significant effect on clutch size. Individual parasitoids oviposited significantly different clutch sizes even when they experienced the same environmental conditions. This result may have been caused by the various nutritional experiences of the parasitoids as larvae. The effect of parasite larval nutrition on adult fecundity was not standardized in order to examine the variability of clutch size in the laboratory colony for use in other experiments. The second factor, parasitoid age, caused the number of eggs laid per ovipositional attack to gradually decrease with time. Finally when hosts were not continuously available,

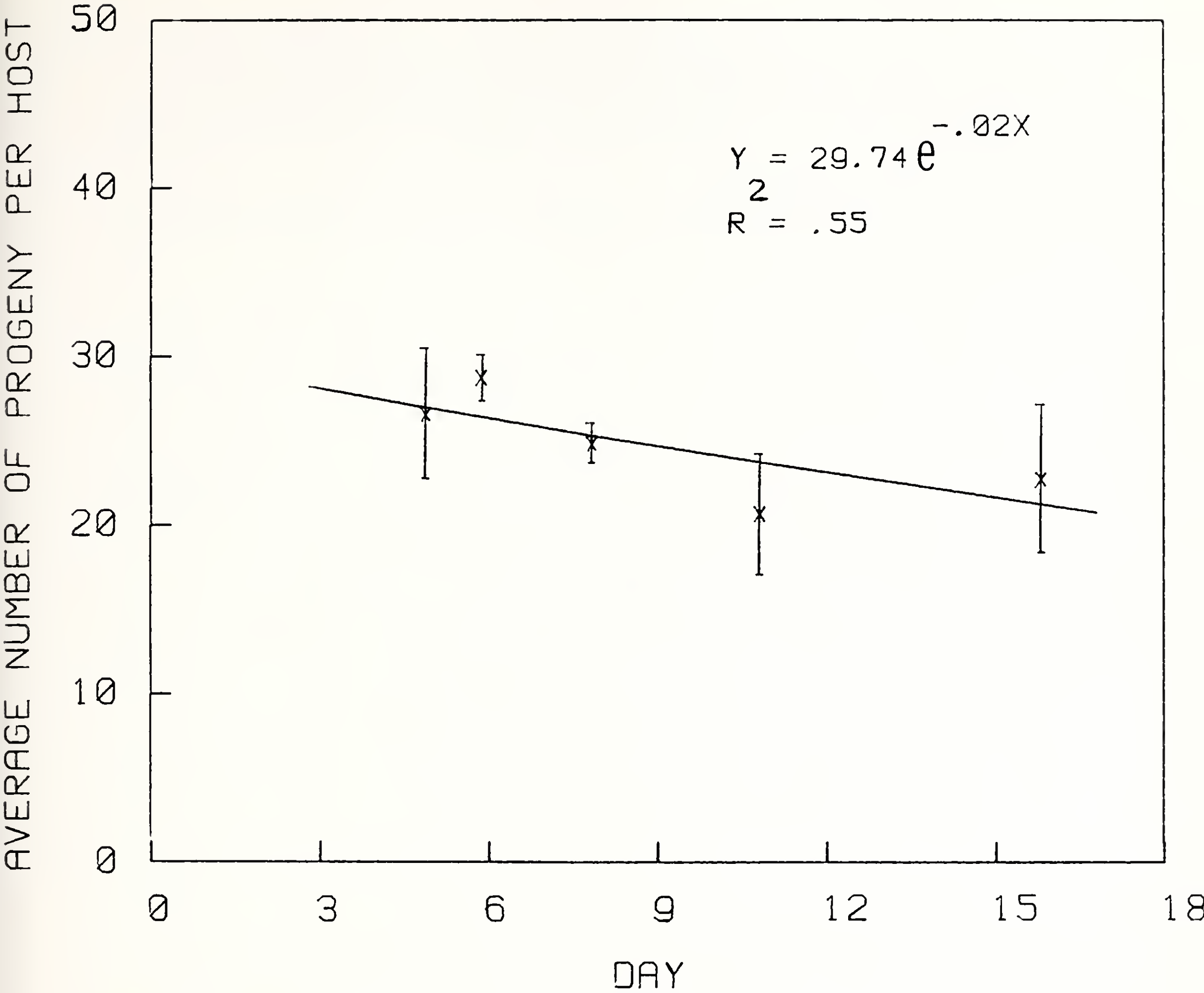

FIGURE 4. *Effect of sporadic host availability on clutch size. The standard error of the mean is plotted for each point.*

parasitoids maintained a high clutch size throughout life. This high clutch size was possibly due to egg storage. Time of day and duration of ovipositional attack had no significant effects on clutch size.

During each ovipositional attack, *M. leviventris* deposits a clutch of eggs whose number varies between individual parasitoids of equal age. As the parasitoid ages, average clutch size diminishes when hosts are continuously available. When hosts are not continuously available, the average clutch size remains high, possibly due to egg storage. For the conditions of these experiments, if the levels of each of these three factors are known, clutch size can be predicted and the number of attacks on a host can be estimated for an individual parasitoid when the attacks are not observed.

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