

HOST FEEDING AND EGG PRODUCTION IN *MUSCIDIFURAX*
ZARAPTOR (HYMENOPTERA: PTEROMALIDAE)

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ABSTRACT

Muscidifurax zaraptor (Hymenoptera: Pteromalidae) is a host feeding synovigenic parasitoid of the pupae of Diptera that breed in animal filth. In a laboratory experiment, we compared the numbers of eggs matured over 3 days by females under three treatments: host feeding on houseflies (*Musca domestica* L.), sugar feeding, and starvation. Starved females resorbed eggs. Host-fed females matured eggs at a constant rate whether they were newly emerged, had been previously starved for 3 days, or had been previously sugar-fed for 3 days. After 3 days of host feeding, females carried approximately 20 mature eggs. Sugar-fed females neither increased nor decreased the numbers of eggs they carried over 3 days, but how many eggs they carry depends greatly on previous diet. No change in the numbers of eggs under sugar feeding occurs because the rates of maturation and resorption are probably equal when hosts are not available for feeding or oviposition.

RESUMEN

Muscidifurax zaraptor (Hymenoptera: Pteromalidae) es un parasitoide de la pupa de Dípteros que vive en desechos de animales. En un experimento en el laboratorio, se comparó el número de huevos madurados por tres días por hembras bajo tres tratamientos: el hospedador alimentándose de moscas (*Musca domestica*), de azúcar, y en inanición. Las hembras en inanición reabsorvieron los huevos. Hembras alimentándose del hospedero maduraron los huevos a un grado constante, ya sean acabadas de nacer, hayan estado en inanición por 3 días, o hayan sido previamente alimentadas con azúcar por 3 días. Después de 3 días de alimentarse del hospedero, las hembras tenían aproximadamente 20 huevos maduros. Hembras alimentadas con azúcar no habían aumentado ni perdido el número de huevos que habían tenido por 3 días, pero el número de huevos que cargan depende grandemente de la dieta anterior. No hubo cambio en el número de huevos cuando se les dio de comer azúcar porque el grado de maduración y reabsorción son probablemente iguales cuando no hay hospederos para comer o poner los huevos.

Female synovigenic parasitic Hymenoptera emerge as adults with only a fraction of the eggs that they mature and oviposit during their lives. In order to mature eggs, synovigenic parasitoids must host-feed by consuming the haemolymph or tissues of their insect hosts (see extensive review by Jervis & Kidd 1986). The synovigenic parasitoid life history contrasts with that of pro-ovigenic species that emerge with their full complement of eggs ready or nearly ready for oviposition. Broadly speaking, host feeding parasitoids need energy and nutrients for maintenance, movement, and egg maturation. Non-host foods, like honey, nectar, or honeydew, may be used before ovaries become mature or when hosts are not available (Flanders 1942, Jervis & Kidd 1986). Host feeding seems to be the primary source of nutrients for egg maturation, while non-host foods are usually used only in maintenance.

Host feeding affects both fecundity and longevity. When deprived of hosts for feeding and oviposition synovigenic parasitoids, like *Nasonia vitripennis* (Pteromalidae), can get nutrition by resorbing mature eggs still in the ovaries (Flanders 1942, Edwards 1954, King & Hopkins 1963, Jervis & Kidd 1986). However, too few synovigenic parasitoids have been studied in the same detail as *Nasonia* to know whether the link between host feeding and egg maturation or resorption is common (Jervis & Kidd 1986).

We report a study of the effect of host feeding on egg maturation in a synovigenic Pteromalid, *Muscidifurax zaraptor* Kogan and Legner, which is native to western North America (Kogan & Legner 1970). This parasitoid attacks the pupae of houseflies, *Musca domestica* L., and other filth breeding Diptera by drilling through the puparium with the ovipositor, killing the host with a venom, and ovipositing on the surface of the pupa (Coats 1976). *M. zaraptor* is solitary (Wylie 1971b, Coats 1976); if more than one egg is laid on a host, the first larva to hatch kills the others with its piercing mandibles (Wylie 1971a). Host feeding occurs after the female inserts her ovipositor into the host pupa—she drinks the haemolymph that exudes from the oviposition hole. However, both females and males will feed on non-host sources like honey or sugared water in the laboratory. Under laboratory conditions females mate once and store sperm, live for up to 53 days, and have a lifetime fecundity of about 210 female offspring at a sex ratio of 21% males (Coats 1976).

METHODS

We obtained houseflies parasitized by *M. zaraptor* from Agricultural Insect Management Inc., Grady, Alabama. Newly emerged mated females were individually isolated in 60 mm by 15 mm plastic petri plates, and kept at 22 degrees C with a 14:10 L:D cycle. Ten females were dissected immediately upon emergence, before feeding. In feeding experiments, three treatments were used: no feeding (starvation), sugar feeding, and host feeding. Sugar-fed females were presented with a sucrose-water solution. Host-fed females received one 1-3 day-old housefly pupa per day.

The experiment was carried out in two parts. In the first part, newly emerged females were either starved, host-fed or sugar fed for three days. The second part of the experiment was conducted on days 4-6, using females that had been starved, host-fed or sugar-fed during the first three days. During this second three day period females that had been previously sugar-fed or starved were host-fed, and females that had been previously host-fed or starved were sugar-fed (see Fig. 1).

The number of fully developed eggs in each female was counted by removing the reproductive tract. Females were killed with ethyl acetate at the appropriate time and were frozen for dissection within the following week. Dissections were carried out under water. While gripping the abdomen at the tip and near the thorax, the entire reproductive tract was gently pulled out. *Muscidifurax* spp. have three ovarioles in each ovary, which is common for solitary pteromalids (Copland & King 1972). Only eggs filled with grayish (dark) material that had the typical "teardrop" shape (Gerling 1967) were counted. The hosts from the host-fed treatment were also dissected, and the number of eggs laid on each pupa were included in the egg counts.

Five to eight females were used in each treatment on each day. The sample size per treatment was determined from the variance of 10 females whose eggs were dissected and counted immediately after emergence (Sokal & Rohlf 1981, p. 263). In all, 148 female parasitoids were used in this experiment.

Data analyses were performed on the total number of "mature" eggs produced by each female. The data were determined to be normal by probability plots, and were found to have homogeneous variance among treatment groups by an F_{\max} test (Kirk

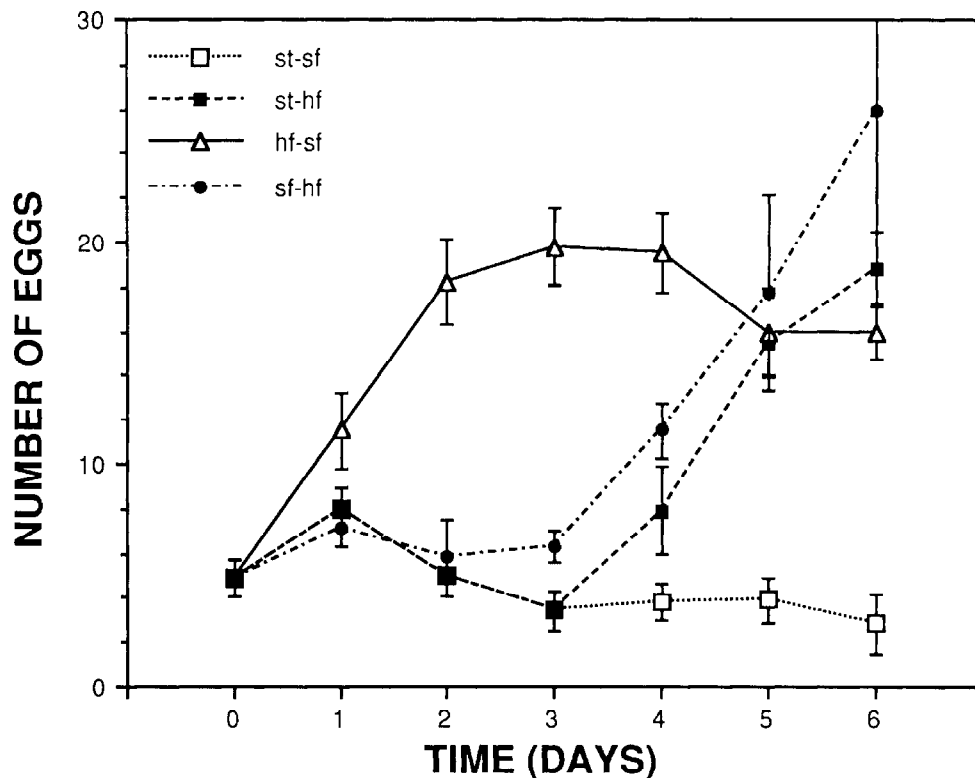


Fig. 1. Plot of the average numbers of eggs matured by females each day of the experiment. Treatment abbreviations are: st-sf: starved during days 1-3—sugar-fed during days 4-6, st-hf: starved during days 1-3—host-fed during days 4-6, hf-sf: host fed during days 1-3—sugar-fed during days 4-6, sf-hf: sugar-fed during days 1-3—host-fed during days 4-6. Error bars indicate standard error.

1982, p. 78). No data transformations were necessary. Regression and analysis of covariance were used to analyze the relationship between the number of mature eggs and time for days 1-3 and days 4-6 of the experiment. F-tests were used to determine whether the slopes of regressions for each treatment were different than zero, and whether slopes differed among feeding treatments (Kirk 1982).

RESULTS

The average numbers of mature eggs produced by females in each treatment group are plotted in Figure 1. Upon emergence, females had 4.9 mature eggs in their ovaries. When starved or sugar-fed during the first day after emergence, females significantly increased the number of mature eggs to 7.5 (t-test: $t=2.59$, 19 d.f., $P<.02$).

Egg maturation by newly emerged females during days 1-3 were compared among the three feeding treatment groups by regression. The slopes of the regressions of egg number on time (the rate of egg maturation or depletion) differed significantly among the three treatments ($F_{2,48} = 12.0$, $P<.001$). Host-fed females increased to an average of 20 mature eggs after 3 days. Sugar-fed females did not have a significant increase or reduction in the number of eggs. Starved females significantly decreased to an average of only 3.4 eggs after 3 days, indicating that some resorption occurred.

We tested whether the rate of egg maturation by host-fed females depended upon previous treatment. We compared the rates of egg maturation by newly emerged females that were host-fed during days 1-3 with maturation rates by females who were host-fed during days 4-6. These second two treatments included females had been sugar-fed or starved for the first three days of the experiment. The regressions from all three groups were significantly positive (Table 1) and slopes did not differ among regression lines ($F_{2,53} = .683$, $P > .50$). This indicates that host-fed females mature eggs at the same rate regardless of previous feeding treatment. Analysis of covariance demonstrated that the average numbers of eggs matured by host feeding females did not significantly differ among females that were newly emerged, that were previously starved, or that were previously sugar-fed ($F_{2,55} = 2.0$, $P > .14$).

A similar comparison was made for sugar-fed females. Egg maturation by newly emerged, sugar-fed females was compared to egg maturation by sugar-fed females who were host-fed or starved for three days prior to sugar feeding. In all three treatment groups, the number of mature eggs in sugar-fed females did not increase or decrease over a three day period, none of the slopes of the regressions differed significantly from zero (Table 1) or from each other ($F_{2,55} = .59$, $P > .55$). Previous feeding treatment, however, strongly influenced the number of eggs carried by sugar-fed females ($F_{2,57} = 84.3$, $P < .001$). Females who were host-fed for three days before sugar feeding had an average of 17.2 eggs, significantly more eggs than females who were newly emerged (6.4 eggs) or females that were previously starved (3.5 eggs) ($F_{1,58} = 155.4$, $P < .001$, by orthogonally contrasts, Sokal & Rohlf (1981, p. 233)).

DISCUSSION

Host feeding is essential for continued egg maturation in *M. zaraptor*. This experiment demonstrates that the nutrition gained during larval development is not sufficient

TABLE 1. REGRESSION EQUATIONS OF NUMBERS OF EGGS (E) OVER THREE DAY (T) PERIODS FOR DIFFERENT PARTS OF THE EXPERIMENT. P-VALUES FOR SLOPES (B) LESS THAN .05 ARE CONSIDERED SIGNIFICANT. IN ALL CASES, THE INTERCEPT (A) WAS SIGNIFICANTLY GREATER THAN ZERO.

Treatment	Regression Equation E = a + bT	r ²	P-value of b	N
Starved for three days days after emergence	E = 9.96 - 2.25T	.43	.003	18
EFFECTS OF HOST FEEDING				
Host-fed for days 1-3 after emergence	E = 8.17 + 4.17T	.40	.005	18
Starved for days 1-3, then host-fed days 4-6	E = 3.07 + 5.55T	.50	.000	21
Sugar-fed for days 1-3, then host-fed days 4-6	E = 4.01 + 7.20T	.31	.011	20
EFFECTS OF SUGAR FEEDING				
Sugar-fed for days 1-3 after emergence	E = 7.28 - 0.42T	.016	.617	18
Starved for days 1-3, then sugar-fed days 4-6	E = 4.52 - 0.50T	.026	.508	19
Host-fed for days 1-3 then sugar-fed days 4-6	E = 20.7 + 1.75T	.087	.161	24

for egg production during the entire adult life. A few eggs were matured by females that were not host-fed during the first day after emergence. When starved, females resorb eggs, but when non-host food (carbohydrate) is available, the number of mature eggs remains constant. This is probably because egg resorption and maturation occur at the same rate when alternative sources of energy are available, a phenomenon found in other parasitoids (Flanders 1942, Jervis & Kidd 1986). The egg maturation rate of 15-20 eggs per day by host-fed females found in this study matches the daily oviposition rate for *M. zaraptor* provided with 20 hosts per day reported by Coats (1976), and is probably close to the maximum. Our study also confirms Wylie's (1971a,b, 1979) standardization technique for *M. zaraptor*. In his experiments on sex ratio and oviposition restraint, females readily oviposited when presented with hosts on the fourth day after three days of honey feeding and host feeding. The importance of standardizing females by host feeding before laboratory experiments is obvious.

Because of resorption, eggs may have a dual function, as units of reproduction and as a sink for nutrients. When hosts are plentiful, many nutrients are shunted to egg maturation, and many eggs can be laid as well. However, if hosts become scarce, these eggs and their nutrients can be resorbed and used for other purposes like dispersal and host searching. Pteromalids like *M. zaraptor* have short oviducts (Copland & King 1972), so that there is little room for storage of mature eggs. Eggs remain in the ovarioles until ovulation and oviposition, and if there are no opportunities for oviposition they are resorbed. The combination of egg resorption and a relatively fast maturation rate after host feeding appears to be a mechanism for taking advantage of unpredictable resources.

Muscidifurax zaraptor females may gain energy from non-host foods such as honey, nectar or honeydew during host-searching without having to resorb more eggs than are matured (cf. Flanders 1942). *M. zaraptor* resorbs eggs one day after emergence if the females are neither host-fed nor sugar-fed. Since resorption has been found to affect attack rates, fecundity, and the sex ratio in other parasitoids (Jervis & Kidd 1986), care should be taken to host-feed, or at least honey-feed, parasitoids like *M. zaraptor* before release for inundative biological control.

The results from these experiments should be viewed with caution when considering the effects of host feeding on population dynamics and host destructive capabilities of this parasitoid. These results extend over only the first six days of life in a species that can live for up to 53 days (Coats 1976). Whether the rate of egg maturation after starvation or non-host feeding is the same later in the life of the wasp should be tested. Furthermore, in this study we tested the effects of feeding regime on the numbers of eggs only. The viability of eggs from host-fed and sugar-fed females may differ. Although early experience did not affect the rate of egg maturation of host-fed females, early starvation may affect longevity. Legner & Gerling (1967) found that *M. uniraptor*, a thelytokous relative of *M. zaraptor*, had greater longevity when deprived of hosts during the first four days of life. Finally, *M. zaraptor* kills 31% of the hosts it encounters without completing development or ovipositing on them (Legner 1979). How the ratio of hosts destroyed to hosts used for oviposition is affected by previous experience and feeding is not known.

M. zaraptor fits the "anhydrotic adaptive syndrome" of synovigenic parasitoids (anhydrotic eggs are those that remain in the ovarioles surrounded by follicle cells until they are ovulated, Jervis & Kidd (1986)). This includes host feeding, the lack of egg storage, few ovarioles (three per ovary), short lateral oviducts, and resorption of unladen eggs. This lifestyle allows considerable flexibility in the allocation of resources to egg production, or to host searching and maintenance.

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