HOST SELECTION BY *TELENOMUS REMUS*, A PARASITE OF *SPODOPTERA LITTORALIS* EGGS

BY

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*Telenomus remus* is an egg parasite of the noctuid *Spodoptera littoralis*. In the laboratory it is not able to find its hosts by smell, as tested in a Y-shaped olfactometer. The parasite female makes “smearing movements” with her ovipositor on the host, after having laid an egg, but she is unable to avoid superparasitism by external and internal examination of the host within the first hour after oviposition. Host eggs that are parasitized when they are 43 hr old or more are doomed, since they do not yield either parasites or host larvae. The parasite female is unable to discriminate between young and suitable hosts, and old unsuitable ones. This last characteristic is considered wasteful in time and progeny.

During a biological study of the scelionid parasite *Telenomus remus* Nixon (Hymenoptera: Scelionidae), we found several characteristics that were different from the ones heretofore known for the family. The following paper reports these findings.

**Materials and methods**

The parasites were cultured on eggs of *Spodoptera littoralis* Boisd. (Lepidoptera: Noctuidae) at 25 ± 1°C and 60—70% R.H. They were reared in plastic petri dishes and were fed honey that was streaked on the lid of the dish. Observations were made through a stereoscopic microscope.

**RESULTS**

*Host finding.* Females of *T. remus* were tested in order to establish if they were attracted specifically to their hosts. This was done with a “Y” type olfactometer in which the parasites were allowed to choose between a tube with a fresh egg batch of *S. littoralis*, and an empty tube. The experiment was run in five replicates in each of which 30 parasites were introduced into the common olfactometer tube (Fig. 1). A constant airflow was directed through the two side tubes (s) into the common tube (c), and the parasites were expected to show whether or not they preferred the side tube with the egg batch over the other.

In all five replicates we got between 14 and 16 parasite females in each of the side tubes, within 5—10 min after the initiation of the experiment, indicating no specific odor attraction. These results were supported by numerous observations of the behavior of adult parasite females of different ages. In all cases, searching
appeared to be at random until the female arrived near the host. Once that happened, her movements slowed down and intense beating with the antennae started, followed by host examination.

**Searching pattern**

Once the parasite female finds the hosts, she mounts them and begins to oviposit. The egg batch of *S. littoralis* usually contains several hundreds of eggs, whereas the *T. remus* female does not lay more than 160 eggs during her lifetime, and a maximum of 60 eggs per day (Schwartz & Gerling, in prep.). Most often the parasite lays in adjacent eggs, but at times she walks over several eggs without ovipositing and commences to lay further on. Her oviposition pattern was followed closely, and analyzed as to the frequency and lengths of the walks that she took from one oviposition to the next. This was done with nine females in order to find out if they exhibited any uniform pattern.
The adjacent egg was stung most frequently, from 50 to 80% of the stinging times. Thereafter followed the next adjacent eggs in a declining succession with only single cases of six to nine egg distances (Fig. 2). The females usually moved onto an unparasitized egg after each oviposition, but occasionally when they passed over an already-parasitized one, they superparasitized it (Fig. 3).

Host recognition and suitability. The behavior of the searching parasite female was examined in order to determine if and how she avoids unsuitable hosts. This was done in respect to two causes of possible host unsuitability, namely superparasitism and host age.

Being a solitary parasite, the *T. remus* female may have a mechanism which enables her to avoid superparasitism. In other species of Scelionidae this is accomplished through the facts that the female marks the host in which she has just laid, and that when she meets a marked host, the parasite female refrains from ovipositing in it (Wilson, 1961; Cumber, 1964; Safavi, 1968).

In *T. remus*, once oviposition was completed, each female was noticed to with-
draw her ovipositor and make a sweeping single motion of some 100—120° over the egg surface. Thereafter, she withdrew her ovipositor and left. On one occasion only, we noticed a female that made three, rather than one, sweeping motions with her ovipositor, and continued to drag it for a short distance in the direction of the former oviposition hole. The significance of these smearing motions, in relationship to superparasitism, was examined in two experiments. In the first, 25 host batches each containing 30 hosts, were allowed to be fully parasitized. Immediately thereafter, the parasite females were removed and each of the batches was introduced into a separate petri dish that contained fresh parasite females. In each case, the fresh parasite females attacked the hosts and commenced to oviposit, as readily and as speedily as they would have done with unparasitized hosts. In the second experiment, a group of *T. remus* females was allowed to oviposit upon 20 hosts, which were then removed and kept apart for 5 min. Thereafter, the hosts and parasites were reintroduced into the same dish and followed closely. Here again, normal oviposition followed and the parasite females did not hesitate or show any behavioral change vs. their normal behavior when laying in unparasitized hosts.

It was therefore concluded that *T. remus* females were unable to recognize previously parasitized hosts by examining their surface, and that the smearing movements performed by the females do not serve for communication in this respect. An exception to this conclusion was noted upon examination of the behavior of the one aforementioned female who performed differently than the rest. In contrast to her sisters, she seemed to recognize eggs in which she had previously oviposited, and refrained from laying in them again. However, she did not recognize eggs that were previously parasitized by her sisters, nor did they recognize eggs that had been marked by her.

We also checked whether or not the parasite female is able to distinguish a parasitized host from an unparasitized one, when she stings it with her ovipositor. It was observed that, once the ovipositor was inserted into the host, it remained there either for 15 sec, or for 37 sec. Dissections revealed that, invariably, the 15-sec insertion was not followed by oviposition and can be referred to as “stinging”, whereas during the 37-sec long insertion of the ovipositor, an egg was laid. This enabled us to determine the outcome of host-parasite encounters without having to dissect each host egg.

Several batches of *S. littoralis* eggs were given to *T. remus* females for oviposition. Once this was accomplished, the hosts and parasites were separated. At 5—10 min intervals thereafter, some of these parasitized eggs were exposed to a group of parasites for oviposition, and the “stinging time” in each case was determined.

It was established that under the experimental temperature of 25°, the parasite females proceeded to lay supernumerary eggs in the hosts for the first 50—70 min following the initial oviposition. Thereafter, stinging lasted only 15 sec and no eggs were laid.

The age of the *S. littoralis* eggs that were parasitized by *T. remus* was found to be critical for successful parasite development. Only hosts that were 42 hr old or
younger ever gave rise to adult parasites. Dissections and histological preparations of older, parasitized hosts showed clearly that the parasite eggs hatched within them, but that the larvae failed to develop. Such hosts died giving rise to neither *S. littoralis* larvae nor to the parasite.

Tests were run in order to establish if the parasite female discriminates between the young suitable hosts, and the old unsuitable ones. For this purpose, two groups of 50 hosts each were subjected to parasitism. One group had 0—42 hr old eggs in it, and the second, 43—70 hr old eggs. This experiment was run in ten replicates and in all cases the parasite’s ovipositional activity was equal for the young and older eggs, indicating no discrimination between the suitable and unsuitable hosts.

**DISCUSSION**

The scelionids exhibit a marking behavior in which they tag the parasitized host. This always involves smearing the tip of the ovipositor upon the host immediately after oviposition. In many cases involving parasites of Hemiptera (Wilson, 1961; Cumber, 1964; Safavi, 1968) and Lepidoptera (Raab, 1970), marking precluded superparasitism to a high degree, saved time and progeny, and enabled the parasites to attack all of the eggs in each host egg batch (Wilson, 1961).

Under laboratory conditions, *T. remus* differs from the above. Although its female performs a smearing motion on the hosts, as soon as oviposition is completed, she is unable to distinguish such hosts from unparasitized ones and superparasitizes them readily. The smearing motion is probably a means for cleaning the ovipositor and, as has been shown in *T. remus*, does not constitute host marking. The latter may have evolved later and is superimposed on the cleaning motions. It involves at least three modifications of the above: more extensive movements of the ovipositor, the emission of a specific chemical, and the ability to perceive and react to such a chemical. Marking of parasitized eggs was apparently needed in order to avoid superparasitism in the cases where the hosts lay their eggs either in small groups or singly. In *T. remus*, a marking mechanism seems unnecessary since *S. littoralis* lays hundreds of eggs in each batch and the number of hosts available for immediate oviposition by the parasite usually exceeds by several fold the capacity of the *T. remus* female to oviposit. Therefore, the chances for natural superparasitism are greatly reduced as is the need for egg marking.

It is conceivable that *T. remus* is either a primitive species, that has never developed marking, or an evolved one, that has lost it. Since no pressures exist to favor the development of marking behavior, and because we found one female that does exhibit it, we must favor the second assumption, namely that *T. remus* has lost the capacity to mark and/or recognize marked eggs.

*T. remus* also fails to recognize hosts that have been parasitized recently (up to 60—70 min previously), after having probed their internal medium, nor is she able to distinguish between young suitable hosts, and older unsuitable ones. We found
no explanation for these characteristics which seem wasteful, since all of the host eggs in each batch are of similar age, and a parasite female that encounters them may spend hours laying eggs that will not give rise to adult parasites.

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RÉSUMÉ

SÉLECTION DE L'HÔTE PAR TELENOmus REMUS, UN PARASITE DE SPOdOPTERA LITtorALIS.

Telenomus remus est un parasite des oeufs de la Noctuelle Spodoptera littoralis. Au laboratoire il n'est pas capable de trouver son hôte par l'odeur, comme le révèle les tests dans un olfactomètre en Y. La femelle de Telenomus marque l'oeuf-hôte avec son ovipositeur après avoir pondu, mais elle est incapable dans l'heure qui suit la ponte, d'éviter le super-parasitisme par examen externe ou interne de l'oeuf hôte. Les oeufs parasités âgés de 43 heures ou plus sont tués, car ils ne donnent ni parasites ni chenilles de l'hôte. La femelle de Telenomus est incapable de distinguer entre des oeufs jeunes et des oeufs âgés, les premiers seuls étant favorables à l'évolution du parasite. Cela entraîne pour le parasite une perte de temps et une réduction de sa progéniture.

REFERENCES


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