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Detection of Mates and Hosts by Parasitic Insects of the Genus *Megarhyssa* (Hymenoptera: Ichneumonidae)

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ABSTRACT: There is a generalized stimulus which attracts the males of *Megarhyssa atrata* (Fabricius), *M. macrurus* (Linnaeus) and *M. greeni* Viereck to form mixed aggregations and to engage in pre-copulatory behavior at the sites of emerging females of any of these species. In addition there is a species-specific stimulus which causes initiation of copulation by males of the same species as the emerging female. The generalized stimulus was identified as the chewing sound made by the female during excavation of her emergence burrow in the wood. The specific stimulus was not identified although sound within the range of 50-15,000 cps and vision were eliminated as possibilities.

The females of these three species can locate accurately the host larvae in the wood and direct their ovipositors to them. The sense involved is either olfaction, detection of sound outside the range of 50-10,000 cps or some unknown sensory mechanism. Females oviposit only on hosts that are at a depth in the wood such that they can just be reached by the ovipositor when it is completely inserted.

INTRODUCTION

The three forms of the parasitic genus *Megarhyssa* to be treated here, *M. atrata lineata* Porter, *M. macrurus lunator* (Fabricius) and *M. greeni greeni* Viereck, occupy similar habitats, overlap in geographic distribution, and are restricted to the same host species, *Tremex columba* (Linnaeus) (Hymenoptera: Siricidae). Indeed, all three can frequently be found active on the same log at the same time.

The broad outline of their life history is as follows: females oviposit after inserting a fine, hair-like ovipositor deep into a log or stump containing the host larvae. After hatching the larvae feed on host larvae and finally pupate within the wood; upon completion of metamorphosis, adults gnaw a tunnel to the outside. Males spend considerable time exploring the surface of logs and can locate the site from which a female will emerge several hours before the event takes place. These males then form aggregations at such sites, and mating occurs as soon as the female emerges.

Two crucial parts of the life history, therefore, are (1) detecting hosts in the wood and directing the ovipositor to them and (2) detecting the presence of females still within the wood. The importance of and difficulties associated with the former are obvious. The latter is important for effecting mating as males will only copulate with a newly emerged female (Abbott, 1934; Harrington, 1887). Conse-

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quently, if males are not present when a female emerges, she is lost to the reproductive resources of the population. We have previously shown (Heatwole, *et al.*, 1963) that there is a generalized stimulus which attracts the males of all 3 species to form mixed aggregations at the site of emerging insects and to engage in precopulatory behavior. In addition there is a species-specific stimulus which causes initiation of copulation by males of the same species as the emerging female. The former operates before the female has made an opening through the surface of the wood; the latter is liberated only after the opening is made. The purpose of the research reported here was to identify these stimuli as well as those involved in host detection by the female. Although this goal was only partly realized, none of us will have opportunity to continue the study in the near future. We feel it desirable to present our results at this time.

The study was carried out in beech-maple forests at Carp Lake (Emmet Co.), and Colonial Point (Cheboygan Co.), Michigan, during the summers of 1958, 1959 and 1960.

The terms used for the various types of behavior such as precopulatory behavior and exploring have been defined in our previous paper mentioned above.

MATERIALS

The following equipment was used in the field during 1960 to study detection of mates: a battery-operated Magnemite 610 E tape recorder (50-15,000 cps response at 15 in/sec) with added pre-amplifier, American Microphone Corp. D-33 A microphone (40-15,000 cps) and Brush BA-200 earphones (100-8,000 cps). The limiting factor for direct monitoring was the earphone response. However, tapes were made and played at one-half speed, thereby dropping the relative frequencies by one-half, and the effective range of the entire system was therefore about 50-15,000 cps. While host detection was studied, a Bell T-203 recorder (response of 20-10,000 cps) equipped with a Stromberg-Carlson MD 57/5535 microphone (60-13,500 cps) with an overall effective response of 60-10,000 cps was used. Direct monitoring with this apparatus was effective only in the range of 60-4,500 cps because of limitations imposed by the headphones.

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DETECTION OF FEMALES BY MALES

The behavior of males aggregated at emergence sites appears identical for all three species. They cluster in a circle around a small area,

bend their antennae and tap the tips rapidly against the substrate (Heatwole *et al.*, 1963). This prominent use of the distal part of the antennae suggests that the sensory organs used in detection of females are located there.

The following account is based on observation of 31 aggregations of males of which 11 were known to be followed by emergences. Female *M. macrurus* and *M. greenei* were observed emerging whereas female *M. atrata* and males were not.

IDENTIFICATION OF GENERALIZED STIMULUS

The generalized stimulus is transmitted through wood. Thus, vision and contact chemoreception are clearly not involved, and the most likely possibilities are olfaction or an auditory sense. Direct monitoring and recording were both employed at aggregations of males at emergence sites. The males dispersed while we placed the microphone against the wood, but they always returned within a few minutes. We listened to emergences attended by males of each of the species studied. Usually 2 or more species were involved in a given aggregation. On all occasions—except one in which we inadvertently killed the emerging female while we were driving the open end of a bouillon can into the wood to insure her capture — sounds similar to those made by a person eating a raw carrot could be heard at the aggregation sites. Such noises were not detected elsewhere in the log, or at the same site following emergence of the female. On one occasion we watched a female *M. macrurus* enlarging the opening of her emergence burrow. Chewing noises, correlating with the movements of her jaws and similar to those heard through the microphone, were faintly audible to the unaided ear.

On 1 July 1960, an aggregation of 6 male *M. greenei*, all performing typical precopulatory behavior, was noted at 1443 hours. We were able to pick up chewing sounds at the site with our apparatus. The males were chased away and the open end of an empty bouillon cube can was driven about 5 mm into the wood at the aggregation site. At 1455 the can was removed. An emergence hole was present and in the can, instead of a female *Megarhyssa*, was an adult pyrochroid beetle (*Dendroides canadensis* Latreille) which had just emerged. On another occasion male *Megarhyssa* were observed aggregating at a site from which this species of beetle subsequently emerged. In still another instance, on 23 July 1960, an aggregation of 8 male *M. greenei*, all engaging in typical precopulatory behavior, was first noted at 1510. The microphone was set in place and the males returned to the site and continued precopulatory behavior, apparently undisturbed by the microphone. Chewing noises picked up by the microphone could be heard throughout the following hour. At 1615 no more chewing sounds were heard and all males left the site. A female cynipoid, *Ibalia scalpellator* Westwood, had partly emerged; her head and part of her thorax protruded from the wood.

Captive males kept in a glass terrarium covered by a board would frequently hang upside down on the underside of the board and rest.

Sometimes scratching on the upperside of the board with a needle would induce precopulatory behavior although at other times no reaction was obtained.

It is clear from the above observations that a chewing sound made by the female in making her emergence burrow constitutes the generalized stimulus which attracts males and induces in them a state of sexual responsiveness. As the chewing noises of all emerging insects to which we listened seemed to us to be the same, it is not surprising that the stimulus does not permit species-recognition by the *Megarhyssa* males.

SPECIES-SPECIFIC STIMULUS

The specific stimulus is not transmitted through wood but is liberated only when a female makes an opening to the surface. At this time a change in behavior of males occurs. Males of the same species as the female initiate copulation. Those of other species leave the immediate site as soon as the chewing noises cease. Only newly emerged females provide the specific stimulus, as is indicated by the observation that when other females, which had emerged some time previously and which were exploring, passed an aggregation of males engaging in precopulatory behavior, they elicited no response even when coming into direct contact with the males. As the visual characteristics of these females were identical with those of newly emerging ones, the specific stimulus does not appear to have a visual basis. When a female had just broken through to the surface, thereby liberating the specific stimulus, males were observed attempting to mount other males, even of different species, indicating that the response of the male is not necessarily directed toward the source of the specific stimulus.

No sounds other than buzzing of wings were obtained with the recorder.

In order to test whether odor was the specific stimulus we conducted the following experiment. On 26 June 1960, a virgin female *M. macrurus* was captured as she emerged. During the night she was kept in a cage at the University of Michigan Biological Station and at 0915 the following day placed in a glass terrarium with a screen top which was then put on the forest floor near a log on which there were active *Megarhyssa* males. Her body was rubbed against two small blocks of wood which were subsequently nailed to logs where *Megarhyssa* males were exploring. The blocks were placed at 1414 and watched through binoculars for most of the afternoon. Males neither formed aggregations on them nor reacted differently to them when their exploratory path happened to cross them. The cage containing the virgin female did not attract males. Odor of this female obviously did not act as a specific stimulus. However, as only newly emerged females stimulate males, it is possible that the female used in this experiment had been out of the wood too long to provide valid results. Perhaps an odor serving as the species-specific stimulus may be lost in the process of hardening of the exoskeleton after emergence. Thus it can be concluded that the specific stimulus is neither visual, nor auditory (at least within a range of 50-15,000 cps); odor, and contact chemorecep-

tion remain as possibilities between which the present study does not permit a definite decision.

Observations on caged animals proved useless, as males of none of the three species showed any response to newly emerged virgin *M. macrurus* females which were placed in their cages on three different occasions. Perhaps the specific stimulus is not effective unless preceded by the generalized one.

DETECTION OF HOSTS

In the past there has been a certain amount of speculation in the literature as to whether *Megarhyssa* females actually detect the presence of host larvae in the wood and whether or not they deposit the egg immediately upon them. Abbott (1934) observed female *Megarhyssa* inserting their ovipositors into open burrows (including one belonging to a buprestid) and believed that they drilled only through bark if at all. He thus concluded that "*Megarhyssa* is not as well equipped with wonderfully mysterious instincts for prey as some students would have us believe." Our observations indicate that *Megarhyssa* females actually detect the host larvae and accurately direct their ovipositor to them. Apparently only those larvae are used which are at a depth in the wood equal to the length of the female's ovipositor. In the more than 100 ovipositions we observed, the ovipositor was always inserted completely into the wood unless oviposition was interrupted by some disturbance. Thus the stimulus must be one permitting directional reception and permitting perception of the depth of the host larva in the wood before insertion.

On 8 July an investigator was stationed near a log in the Colonial Point study area where numerous *Megarhyssa* were active. Females were watched through binoculars during oviposition and when the ovipositor was inserted, the investigator cut it off at the base with a scissors, marked the spot on the log with paint, and preserved the female. Three such places with ovipositors *in situ* were marked within 3½ hours, after which the log was transported to the laboratory and sawed into sections at the oviposition sites.

None of the ovipositors followed burrows or cracks the entire way; all penetrated firm wood. One female *M. atrata* began oviposition in an old emergence burrow but when the burrow turned at a depth of about 2 cm the ovipositor continued straight through the intact wood. At a depth of 5.5 cm the ovipositor also successfully penetrated a core of hard wood until its entire length had been inserted. When the log was sawed open, the tip of the ovipositor was found to be 2 mm above the posterior end of a host larva. As the female had begun to withdraw the ovipositor when it was cut off, it is probable that it had been at least 2 mm deeper at maximum insertion, and had therefore penetrated the cavity containing the host.

One of the female *M. macrurus* had initiated insertion in an old emergence burrow which was filled with fungal hyphae. The ovipositor passed through it into firm wood. The ovipositor was cut off during a late stage of insertion and the tip found to be 9 mm directly above the

center of a cavity containing a host larva. This can be considered an accurate placement, for there was still 9 mm of ovipositor protruding above the surface of the log. Complete insertion would have placed the tip of the ovipositor just within the cavity containing the larva.

The ovipositor of a second female *M. macrurus* was cut off during insertion. The ovipositor was 86 mm long, 74 mm of which had been inserted. The tip was 12 mm above the anterior end of a host pupa 30.5 mm long and would have entered the cavity containing the host if complete insertion had been permitted. At a depth of 6.6 cm the ovipositor passed completely through an old, frass-filled *Tremex* burrow. The point of entry of the ovipositor into the log was in firm wood.

These observations indicate that not only does *Megarhyssa* detect the host in the log with sufficient accuracy to deposit an egg directly within the cavity containing it, but that it does so without necessarily following either the burrow of the host or naturally occurring crevices. Insertion of the ovipositor into old burrows seemed to be fortuitous and to have simply resulted from their being located between the female and the host she had located. The path of the ovipositor was always straight and never deviated from its course as a result of passing into or through old tunnels. It is important that the egg is deposited directly within the cavity containing the host. The host larvae are completely encased in wood except for the burrow behind them which is packed with frass. Cushman's (1926) suggestion that *Megarhyssa* merely oviposits in a *Tremex* burrow and that the parasite larva crawls through it to the host is untenable because of the hard, almost woody consistency of the frass packing the burrows, and the weak mouthparts of larval *Megarhyssa*. Furthermore, ovipositing females observed in the present study were sufficiently accurate for direct placement.

The manner in which distal parts of the antennae are used during host and mate detection (Heatwole *et al.*, 1963) suggests that the sensory organs involved in both processes are located near the tips of the antennae.

We had little success in discovering the mechanism of host detection although several sensory systems were eliminated. Sound resulting from the chewing of wood by the host larvae is probably not involved as in one instance recorded here, upon opening a log, an ovipositor of a *M. macrurus* female was found to be directed toward a *Tremex* pupa, a stage which remains stationary and does not chew. Also no sounds could be detected through the microphone anywhere on the log (including places where female *Megarhyssa* were ovipositing) except where insects were emerging and hence chewing near the surface. For obvious reasons, vision, tactile receptors and contact chemoreception are not involved.

Olfaction and ultrasound are possibilities although it is difficult to see how the former could be used to locate directionally the host so precisely through such a thick layer of wood. Exploring females paid no attention to parts of the log upon which we had rubbed the body of a host larva, nor to those upon which we had smeared a smashed larva, even though their paths fortuitously crossed such places. Ultra-

sound produced by the host and detected by the parasite, unless it fulfilled some vital function for the former, might be strongly selected against and hence is probably not operating here. Ultrasound produced by *Megarhyssa* and used for echolocation of host larvae is a possibility which was not explored in this study.

Whatever the method of detection, females cannot distinguish whether the larva they have located is already parasitized before drilling down to it. One of the females discussed above had directed her ovipositor to an already parasitized *Tremex* larva. However, it is possible that sensory receptors on the ovipositor might prevent dual parasitism by relaying information after contact with the host, as had been suggested for *Trichogramma* by Salt (1937).

An experiment designed to evaluate the role of the ovipositor in host recognition was set up. An abdomen of a female *M. macrurus* was cut off and mounted alive on a paraffin block after the method of Dethier (1947). The tip of the ovipositor was tested for its reaction to a water suspension of a macerated host larva and as a control to distilled water. It reacted to both by contraction of the abdominal muscles and an occasional sideways motion of the posterior part of the abdomen. Hence, no information on the role of the ovipositor as an auxiliary sensory organ was obtained.

The change in pressure upon the tip of the ovipositor when it enters the cavity of the host larva may supplement the host-detecting senses in establishing when contact has been made and the eggs should be released. However, the passing of the ovipositor of a *M. macrurus* female through an old (albeit frass-filled) burrow did not influence ovipository behavior.

DISCUSSION

The problem of orientation of *Megarhyssa* with respect to mates and hosts has only partially been solved. The results of this study indicate that the generalized stimulus, i.e., that stimulus which attracts males and stimulates them to aggregate and carry out precopulatory behavior at future emergence sites of a female, is the chewing sounds she makes while excavating her emergence burrow. However, whether this is received as a true auditory stimulus or a vibration of the substrate is still to be determined. The specific stimulus, i.e., that stimulus which causes the males of the species corresponding to that of the emerging female to initiate copulation, has not been identified although all known senses except olfaction, contact chemoreception and response to sound outside the range of 50-15,000 cps were eliminated.

Similarly, all known senses were ruled out as not being involved in detection of host larvae except olfaction and reception of sound outside the range of 60-10,000 cps. That either of these two senses may be involved is not contrary to available information on antennal sense organs of this group, although such information is still rather fragmentary. Dr. Eleanor Slifer has histologically examined the antennae of *Megarhyssa* and informs us (personal communication) that there are present two types of hairs (probably olfactory) and also

plate organs. The function of plate organs is not certainly known, although Slifer and Sekhon (1960) suggest, on the basis of electron microscopical examination of these organs in the honeybee, that they may be detectors of sound or some other vibratory stimulus. However, the possibility that they are olfactory or even light receptors has not been ruled out (Slifer and Sekhon 1961).

Evidence has accumulated which attests to the importance of sound and/or substrate vibrations to Hymenoptera. For example, Lindauer and Kerr (1960), in working with communication in stingless bees, found substrate sound important in information exchange between workers. More recently, Wenner (1962) has shown that information is transmitted through the substrate from one queen honeybee to another.

A related problem to that of how mates and hosts are located within logs involves the finding of the log. Abbott (1936) removed the antennae from some marked males of *M. lunator* (= *M. macrurus lunator* of present nomenclature) and noted that they subsequently returned to the log on which they had originally been captured, even after a period of several days, thereby indicating that the antennae are not necessary for finding the log, at least after it has once been visited. However, his conclusions that "the antennae of *Megarhyssa* are of doubtful value in bringing about mating" and that "the function of these antennae as olfactory organs is also doubtful" are rather puzzling and not warranted from the fact that antennectomized males returned to the same log. Our observations indicate that the antennae are of great importance in bringing about mating.

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