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The Behaviour of *Megarhyssa*, a Genus of Parasitic Hymenopterans (Ichneumonidae: Ephialtinae) ¹

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With 3 Figures

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Introduction

The life cycle of *Megarhyssa* begins when the female inserts a hair-like ovipositor deep into a log or stump and deposits an egg. The larva feeds on immature wood-boring insects and after pupation in a burrow, metamorphoses and chews out of the log. Adult males are able to detect the presence of a female in the wood and aggregate on logs or stumps around future emergence sites. They are on hand at the time of the female's appearance; mating takes place immediately. The inseminated female later completes the cycle by ovipositing in wood.

The three species treated here, *Megarhyssa macrurus lunator* (Fabricius), *M. atrata lineata* Porter, and *M. greeni greeni* Viereck, are large ones reaching 3—4 cm in length (excluding ovipositor). They are "good" species morphologically and owing to a recent revision of the genus by TOWNES and TOWNES (1960), their systematics and distribution is well known. All three are closely related and appear to inhabit the same ecological niche, as they overlap in geographical range, occur in the same habitat, and are commonly found together on the same log or stump. They are even restricted to the same host, the pigeon tremex, *Tremex columba* (Linn.), a horntail (Hymenoptera: Siricidae) whose immature stages inhabit dead wood.

These conditions suggest a violation of the principle of competitive exclusion (HARDIN 1960) and raise certain questions concerning the mechanism effecting reproductive isolation. Further difficult problems are the methods

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employed by males in detecting the presence of females in the wood, and that used by the females in finding host larvae. A detailed description and analysis of the behaviour of all three species is essential for the solution of these and related problems.

During the summers of 1958, 1959, and 1960, a study of biotic interactions, reproductive isolation, and detection of hosts and mates in these ichneumonids was carried out in beech-maple forests at Carp Lake (Emmet Co.), Michigan, and Colonial Point (Cheboygan Co.), Michigan, USA. This paper presents a description of their behavioural patterns and is expected to provide a basis for forthcoming reports on other aspects of the study.

Methods

The chief method employed was direct observation of the insects on logs in their natural habitat, although supplementary observations were made on caged individuals. All three species are large enough to be identified and their sex readily ascertained from a considerable distance with the aid of 7×50 binoculars, a method which permitted observation and taking of field notes without disturbing the animals. On several occasions when closer observation was employed, it was found that if the investigator remained motionless for a few minutes the insects would resume their usual activities.

Exploratory Behaviour

Most of the activity of insects at logs consisted of alternation of two types of behaviour which will be termed exploratory behaviour and resting, even though the latter may be more involved than indicated by the term applied. Exploratory behaviour appeared identical in all three species and although playing a different role in the male (finding of mates) than in the female (detection of hosts), was superficially the same in both sexes. The following will serve to outline exploratory behaviour for all three species.

The insects walk slowly over the log or stump moving their antennae alternately up and down. The antennae are slightly divergent and enclose an angle of about 45°. They curve slightly downward and at about three-fourths of the distance from the head, bend abruptly toward the substrate so that as they are moved, only the extreme tips are tapped against the substrate. The animal may occasionally stop and tap the tips of the antennae alternately (or rarely synchronously) on the substrate, touching the wood at a slightly different location each time. This results in an intensive investigation of a small area as compared to the larger area less completely covered while walking. Movement of the antennae is more rapid at such times than it is when the insect is walking. Following investigation of a small area, the insect may resume walking, assume the resting position, or if a suitable stimulus is received, become engaged in oviposition or other behaviour patterns, depending on the sex of the animal and the nature of the stimulus.

When an insect receives a stimulus (indicated by its stopping and exploring) at a particular spot, it frequently returns to the vicinity a number of times for repeated intensive exploration. Otherwise movement over the log does not seem to follow any particular pattern (Fig. 1).

Some exploration commonly occurs before an insect alights on the log or stump. Both sexes have been observed flying erratically back and forth with the antennae extended to reach a zone about 2 cm above the surface of the log.

The females appeared to spend proportionately more time exploring than did males. The former explored almost constantly, stopping infrequently in the resting position and then only for 2—5 seconds (Fig. 1). By contrast males

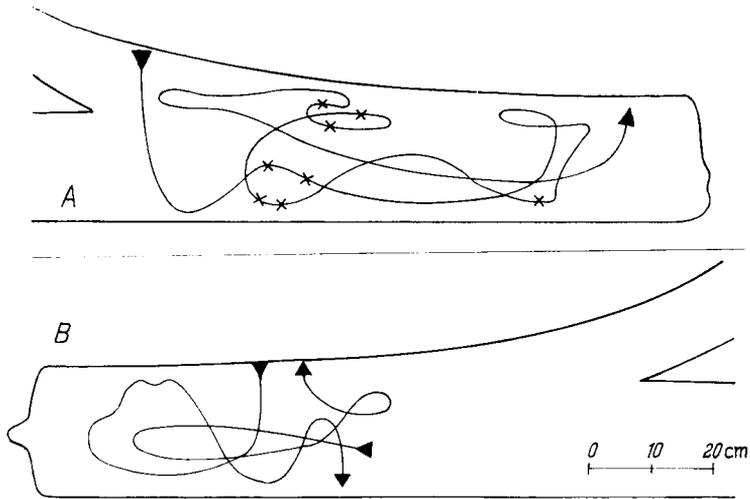


Fig. 1 A. Exploratory route of a female *Megarhyssa atrata* on a dead log, 30 June 1960. Arrows at beginning and end of route show direction of movement. X's indicate sites where she stopped to explore intensively for 3–5 seconds. B. Same for 2 different female *M. atrata* on 9 July 1960. Stops not recorded

spent much of the time in the resting position. On several occasions, the activities of male *greenei* were timed. Of the total observation time of 35 minutes, only 66 seconds (1.7%) were spent in exploratory behaviour. On other occasions, males of this species have been observed resting in the same position for as long as 10 minutes. Corresponding activity periods for a male *macrurus* and a male *atrata* were 37 seconds out of 5.5 minutes (11.2%) and 4 seconds out of 9.5 minutes (0.7%), respectively.

An additional behavioural pattern called “dipping” was occasionally employed during periods of exploration. Males would curve their abdomens down and rub the tip against the substrate for several centimeters as they walked along. The parameres were spread out with their ventral surfaces against the wood. Male *greenei* performed dipping frequently whereas those of the other two species rarely did. It was never observed in females.

Sexual Behaviour

The pre-copulatory behaviour of all three species is identical. At the sites from which a female is about to emerge, males aggregate in groups and all face inward around a circular area 5–30 mm in diameter. They bend their antennae and tap them in exploratory fashion but at a much more rapid rate than during ordinary exploring. Each male frequently shifts position in the circle, and if many are present they will sometimes climb over each other. During this period of antenna tapping, they bend their abdomens sharply down and forward under the thorax so that the tip contacts the substrate at the same spot as their antennae. This behaviour continues until the female emerges, whereupon mating immediately takes place.

If there are small holes or crevices present in the wood near the place where the female is emerging, an additional type of pre-copulatory behaviour occurs. The males gradually force their abdomens into these small holes, sometimes all the way to the thorax. In this position the first pair of legs sometimes

fail to make contact with the substrate. Occasionally several (up to four) males have their abdomens inserted into the same hole. They have the ability to utilize what seem to be excessively small holes. On one occasion a male was observed to tear his abdomen in two while trying to extricate himself. When the female breaks through the surface of the wood, males may insert their abdomens into the emergence burrow. Previous speculation as to the function of this practice includes the supposition that the males are trying to enlarge holes to help females emerge (FATTIG 1949), a view not substantiated by our observations. HARRINGTON (1887), GADE (in BARLOW 1921), and CHAMPLAIN (1921) felt that females may be inseminated before they emerge from the wood. Although this behavioural pattern appears to be related to copulatory behaviour and is elicited only when males are in a state of sexual responsiveness, it is questionable whether insemination of females is ever accomplished in this way. The females' abdomens are longer than those of the males, a factor which might effectively prevent the genitalia from coming into contact in the burrow. The normal copulatory position used above the surface of the wood (see below) also militates against the acceptance of HARRINGTON's interpretation.

Behaviour of *atrata* males in aggregations differed slightly in that they did not try to insert their abdomens into small holes although the abdomen-bending behaviour so characteristic of *greenei* and *macrurus*, was observed.

We observed copulation only in *macrurus*. Our observations, summarized below, agree in all essentials with the description of mating in this species given by ABBOTT (1934a). As the female came out of the wood, two males attempted unsuccessfully to insert their abdomens into the hole through which she was emerging. A third mounted her backwards, clasping her thorax with his legs. After she had completely emerged, he released his hold, turned around and mounted her abdomen, this time facing the same direction as the female. He clasped her abdomen with all three pairs of legs and then using the posterior pair, stroked her abdomen on the underside. At first the female vibrated her wings but later became motionless. The male curved his abdomen around on the left side and underneath her, finally orienting so that his abdomen was in a semicircle with the genitalia facing backward and contacting the anteriorly directed genitalia of the female. The male's claspers (parameres) were widely spread, one pressing against each side of the female. The pair remained in this position for 5 minutes after which the female vibrated her wings several times and pushed her posterior pair of legs against the male, sometimes getting a leg between her abdomen and the male and pushing laterally. The male crawled forward over her thorax and then to the left, at the same time straightening out his abdomen. The abdomen of the female was pulled forward until, after three attempts, their genitalia became unfastened, allowing her abdomen to regain its usual position. The process of dismounting occupied 3 minutes.

During this emergence several males attempted to mount other males in the copulatory position but were unable to do so because of the strugglings of the latter. One *macrurus* male attempted to mount an *atrata* male that was exploring in the vicinity. Homosexual mountings were also observed on other occasions among *atrata* males.

While engaged in pre-copulatory behaviour, males do not respond to certain stimuli to which they usually react. They can be approached and even picked up in the hand before they attempt to fly away or otherwise alter their behaviour.

Size of aggregations range from several individuals to more than 10. Prior to the time the female breaks through to the surface they are usually composed of more than one species (Table 1) suggesting that at this time the

Table 1. Composition of aggregations of males at emergence sites where the female had not yet made an opening to the surface of the wood.

Date	Number of males in aggregation			total
	<i>atrata</i>	<i>greenei</i>	<i>macrurus</i>	
3 July 1959	3	3	0	6
25 June 1960	0	1	3	4
26 June 1960	0	5	2	7
27 June 1960	1	5	0	6
28 June 1960	0	9	2	11
1 July 1960	0	6	0	6
5 July 1960	0	7	0	7
11 July 1960	1	2	0	3
23 July 1960	0	8	0	8

males are receiving some generalized stimulus which attracts them to the site but which does not permit them to discriminate between different species of females. Later, however, when an opening has been made, species recognition is possible, presumably due to the release of a species-specific stimulus which cannot be transmitted through wood. This stimulus causes males to initiate copulation.

On 29 June 1959, an aggregation of 4 *macrurus* males was observed. At the time it was first observed, a small hole was already present in the wood and the insects were engaged in typical pre-copulatory behaviour, rapidly exploring the site with their

antennae and attempting to insert their abdomens into the emergence burrow. During the 1½ hours they were observed, 2 male *greenei* and 2 male *atrata* came up to the aggregation and explored the emergence burrow for several seconds and then immediately left without bending their abdomens or showing any other pre-copulatory behaviour. They resumed exploring on other parts of the log. Two other *greenei* and 2 other *atrata* which were exploring on the log did not approach the aggregation of *macrurus*.

All single-species aggregations at places where the female had not yet broken through to the surface were composed of *greenei*. Males of this species were much more abundant than those of the other two, and the lack of *atrata* and *macrurus* in such aggregations was probably the result of chance.

Oviposition

The unusual method of oviposition of *Megarhyssa* has been commented upon in the literature (RILEY 1888, FYLES 1916, FATTIG 1949 and others). BAUMANN (1923) and ABBOTT (1934b) published detailed descriptions of the anatomy of the ovipositor and associated parts of the female's abdomen in several species of this group. However, a complete description of oviposition is lacking for any one species and no attempt has been made to compare the methods used by different species.

All three species begin oviposition only after considerable walking and exploratory behaviour, followed by more intensive exploration of a single spot while remaining stationary. This apparently functions as an aid in host detection. In the present study 83 complete or partial ovipositions of *atrata* were observed with corresponding values of 28 and 32 for *macrurus* and *greenei* respectively. The methods used by the former two were essentially identical but parts of the process differed somewhat in *greenei*. Several females did not appear to be disturbed by the investigators' presence while ovipositing and could be watched from only a few inches away and even examined with a hand lens.

The following account, illustrated by figures 2 and 3, will serve to describe the process in *atrata* and *macrurus*. Insertion of the ovipositor is effected by raising the abdomen vertically and then bending the tip in such a manner that the ovipositor swings forward (Fig. 2 A, B). As the ovipositor is too long for

the tip to swing into drilling position it is necessary that part of the length be taken up by some means. This is accomplished by expansion of the conjunctival membrane between the 7th and 8th terga and the membranous ventral body wall (SNODGRASS 1935). These membranes will be collectively called the ovipository membranes and are shown in Fig. 2 C and 3 A. The terminal segment of the abdomen is bent downward and the posterior part of a compound structure called the "drilling organ" (Fig. 2) turns clockwise (when viewed from the left side) through 360° . As this occurs the ovipositor passes between the 7th and 8th abdominal segments, stretching the ovipository membranes out through the dorsal surface. When this movement is complete,

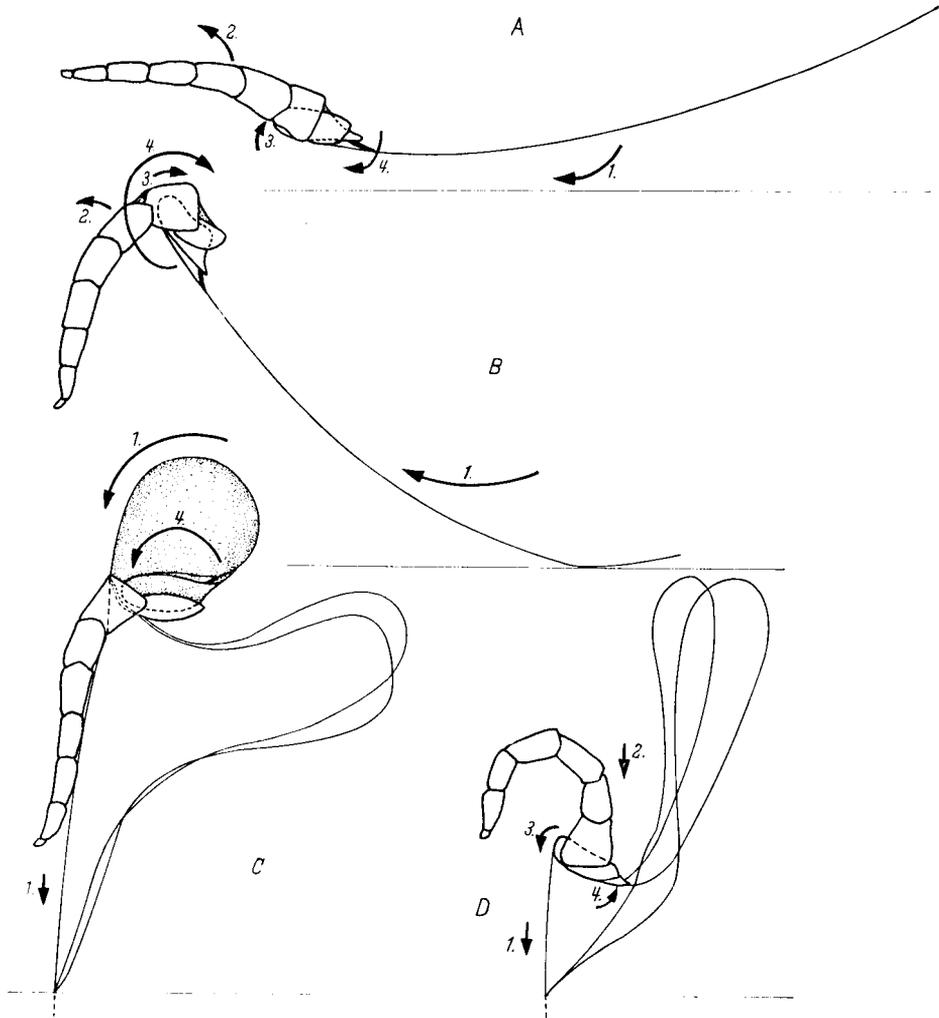


Fig. 2. Diagrammatic representation of successive positions of abdomen and ovipository apparatus during oviposition by a female *Megarhyssa atrata*. Arrows indicate direction of movement of (1) the shaft of the ovipositor, (2) the abdomen, (3) the anterior end of the drilling organ and (4) the posterior end of the drilling organ. The ovipository membranes are shaded; that part of the drilling organ and ovipositor not externally visible is represented by dotted lines

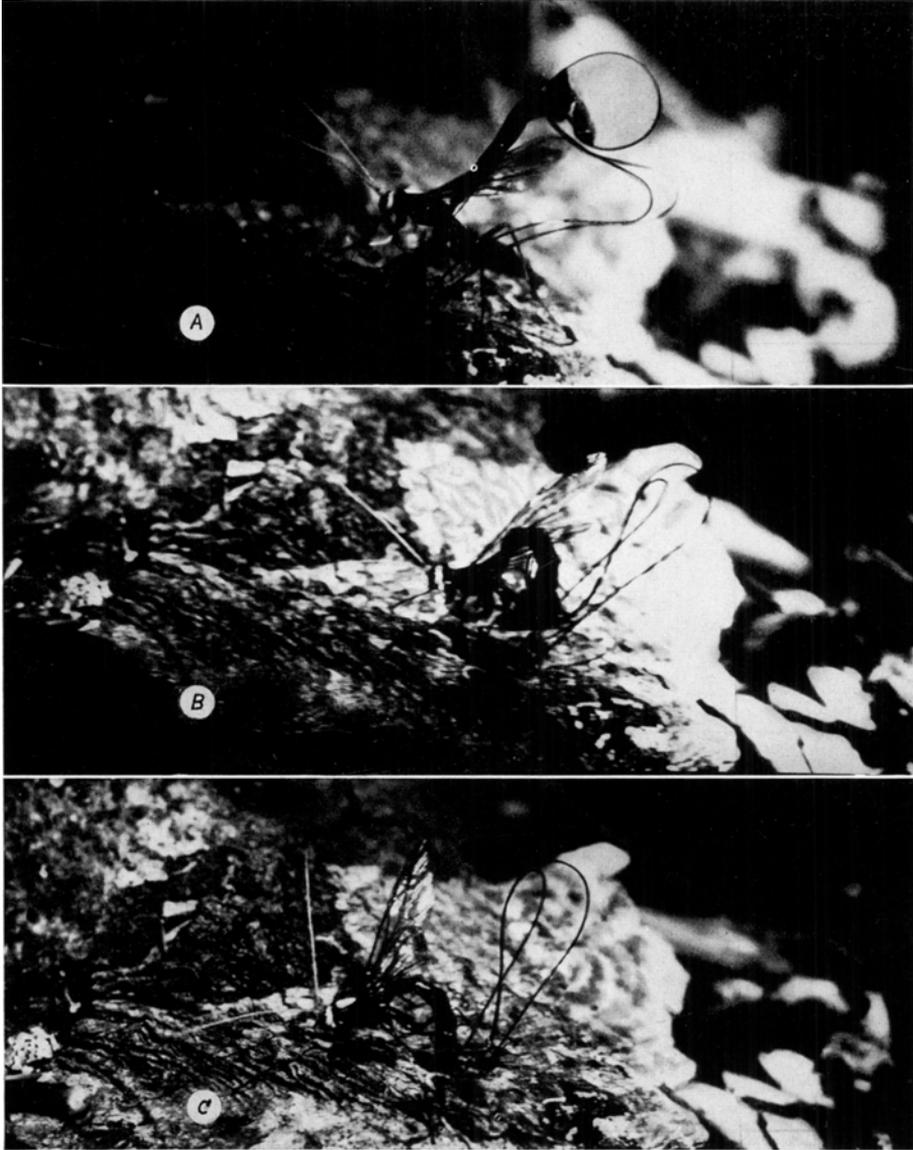


Fig. 3. Successive stages of oviposition by *Megarhyssa atrata*. A. Expansion of the ovipository membranes and placement of the ovipositor. B. Inserting ovipositor. C. Completion of insertion

drilling organ is up-side-down within the membranes and the ovipositor forms a loop keeping the membrane taut (Fig. 2 C, 3 A). The circular movement of the drilling organ is accompanied by periodic, anteriorly directed movements of the vertically oriented abdomen. Each time the abdomen is moved forward, the end of the ovipositor catches on the rough surface of the substrate and as the muscles of the abdomen relax again and the abdomen moves backward, a force is applied along the ovipositor which undoubtedly aids in expanding the membranes. When the loop of the ovipositor within the membranes is

sufficiently large that the tip of the ovipositor touches the wood directly beneath the thorax, much of the length of the ovipositor comes to lie in a groove on the ventral side of the abdomen. Insertion is accomplished by rhythmic contraction and relaxation of the muscles operating the drilling organ although pressure applied by the taut membranes undoubtedly aids in this process. After each contraction, the sides of the abdominal groove clamp against the ovipositor, keeping it in position during the subsequent relaxation of the muscles of the drilling organ. At this stage of insertion much of the length of the ovipositor is still outside the wood and it would be quite easy for it to buckle under the pressure applied were it not for the abdominal groove maintaining it in position.

The ovipositor is composed of a central shaft (in turn made up of 2 fused valves and 2 lancets) attached to the anterior end of the drilling organ and 2 "guides" (third valvulae) attached to the posterior end (ABBOTT 1934b, SNODGRASS 1935), the latter joining each other to enclose the central shaft in a sheath. The central shaft is invariably inserted completely into the wood whereas the guides penetrate only a short distance if at all, and form a supporting tube for the shaft at its point of entry into the wood. The remainder of the length of the guides form large loops posterior to the insect (Figs 2 C, D; 3 B, C). Drilling, according to ABBOTT (1934b), is accomplished by lateral movements of 2 pairs of plates of the drilling organ which in turn move a third pair. The lancets of the shaft are attached to the latter, and are alternately activated by their movements. The lancets are grooved and slide along a pair of T-flanges on the fused valves.

Movement of the drilling organ continues until it is back to its normal position again and the ovipositor is inserted far enough that the ovipository membrane is completely contracted. Progressive arching of the abdomen, accompanied by rocking movements of the drilling organ (Fig. 2 D, 3 B), applies a downward pressure on the ovipositor and drives it deeper into the wood. The relative importance of the "drilling" brought about by movements of the lancets, and the application of force upon the shafts of the ovipositor by the abdomen and ovipository membrane was not ascertained.

The shaft is a very fine, hairlike structure; yet it is inserted in some instances as deeply as 10 cm or more. On occasions when a female was killed during oviposition and her ovipositor cut out of the substrate, the wood was found to be quite firm. The ovipositor was not located in a crack or burrow as suggested by ABBOTT (1934a).

The process of extracting the ovipositor is simply the reverse of insertion and if the arrows representing movements applying force are reversed in Fig. 2 and the drawings studied in reverse sequence, a good idea of the process can be obtained. However, the guides are usually not included inside the ovipository membrane during extraction whereas they usually are during insertion. When the ovipositor is completely free from the wood and the ovipository membrane at maximum expansion, the abdomen is extended forward over the thorax allowing the ovipositor to swing backward during the rapid circular motion of the drilling organ and contraction of the ovipository membrane which follows.

The differences in oviposition which are found in *greeni* result chiefly from its short ovipositor in relation to its body length. Sometimes the ovipository membrane is used as described above for *atrata* and *macrurus* but more often it is not. The abdomen is raised, the ovipositor swung into position

immediately by bending the tip of the abdomen. Pressure is then applied in the same manner as in the other species after the ovipositor has penetrated far enough that the membrane is not in use.

A great difference was found between species in length of time required to complete oviposition. Five complete ovipositions of *atrata* averaged 1 hour and 7 minutes (range: 22 min.—5 hr., 33 min.). All but one took more than one hour. The corresponding value for *macrurus* (N=2) was an average of 12 minutes (range: 5—19 min.). *Greenei* (N=4) averaged 7.5 min. with a range of 4—11 min. Length of time necessary for oviposition is related to ovipositor length; *atrata* has the longest ovipositor and *greenei* the shortest, with *macrurus* being intermediate.

The use of the antennae during oviposition varied among individuals. The most common pattern for all species was to bend them down and back under the thorax during initial placement of the ovipositor and rapidly tapping the area in which the ovipositor was to be inserted. After the ovipositor was in place and beginning to penetrate the wood, the antennae were usually held motionless, divergent and slightly raised (Fig. 3). This position was usually maintained throughout the rest of the oviposition. However, when a female would make an unsuccessful attempt to sink her ovipositor in the wood, each time withdrawing it part way and then inserting it again, the antennae were used in the same manner as during the original placement. Still less frequently the antennae continued moving during the entire oviposition and in two instances, *macrurus* females were observed to hold one antenna down against the wood and the other in the air at right angles to the axis of the body.

Grooming Behaviour

Under this category will be considered all types of behaviour which function in cleaning the body parts or keeping them in order. This type of activity is often elicited by the presence of foreign material on the body or improper alignment of some part. Usually it is of short duration, lasting only 5—15 seconds. However, on one occasion a male *atrata*, which had recently been marked with paint, groomed continuously for 17 minutes. A captive, newly emerged female *macrurus* groomed intermittently for several hours.

Antennal cleaning was repeatedly observed in both sexes of each of the species except for female *greenei*. The behaviour is identical in all of them and followed a rather stereotyped pattern. One of the legs of the first pair is lifted and placed on top of an antenna and then lowered, thereby pulling the antenna through the angle of the joint between the femur and tibia. The same procedure is then repeated using the leg and antenna of the opposite side of the body. Commonly opposite antennae were alternately groomed several times in succession.

Grooming of the first pair of legs, observed in male *atrata* and female *macrurus* and *greenei*, is identical in all species. The leg on one side is lifted and then with a slight rotation of the head it is taken between the mandibles which move gently back and forth as the leg is drawn between them. This is then repeated using the opposite leg.

Grooming of the second and third pairs of legs occurred less frequently. The former was observed only in female *macrurus* whereas the latter was observed in males of all three species and in female *macrurus*. The females lift the first pair of legs and stroke the second and occasionally the third pairs

by applying the medial surface of the first pair to the lateral surface of the others and moving downward along them from the proximal to the distal part. This was usually repeated several times. The third pair of legs was more commonly groomed by lifting them, crossing them and then rubbing them together by moving them alternately back and forth. This was the only method seen to be employed by males.

The third pair of legs are not only used to groom each other but the wings, abdomen, and ovipositor as well. The wings are held backward above the abdomen and the third leg lifted and placed in contact with them. The legs are bent at the joint between the femur and the tibia and then extended, moving the tibia backward along the edge of the wing. The wings of both sides may occasionally be groomed simultaneously. This behaviour was observed in males of all three species and in female *macrurus* and *greenei*. An additional behaviour pattern was observed once in a male *atrata* which used the second pair of legs in conjunction with the third pair.

In female *macrurus* and *greenei* the abdomen is groomed in very nearly the same manner as the wings, i. e., the legs of the third pair are lifted and bent and then rubbed posteriorly along the side of the abdomen as they are extended. The abdomen is simultaneously curved in an arch bringing the posterior part forward to meet the legs. In male *greenei* the process sometimes differs in that the abdomen may be elevated and lowered during grooming. In male *atrata* there are two types of behaviour, that listed above for female *macrurus* and *greenei* and an additional one in which the posterior pair of legs is extended above the abdomen where the legs are crossed. The abdomen is sharply curved downward and the legs work their way by alternate movement, backward along the top of the abdomen.

Grooming of the ovipositor was observed many times in females of *macrurus* and *atrata* but never in *greenei*. In *macrurus* the third pair of legs is extended above the abdomen and then crossed. The abdomen is then lifted upward, curving at the tip, and finally bent forward above the rest of the body. This draws the ovipositor between the legs. As mentioned previously, the guides of the ovipositor become separated from the shaft during oviposition. If they do not automatically assume their former attachment to each other after oviposition, grooming of the ovipositor takes place and may occur several times until the correct orientation of parts is restored.

In *atrata* the grooming of the ovipositor is identical except that sometimes the legs are not crossed but are simply held tightly together and the ovipositor drawn between them. The angle of elevation of the abdomen varies. It is almost always 90° or more. On one occasion a female *macrurus* after lifting its abdomen extended it anteriorly over its head until it was only 1 cm above the surface of the log.

Resting

The insects intersperse exploration with periods in which they remain motionless. The position assumed when at rest is the same in all three species. The abdomen is slightly raised and usually somewhat curved; the wings are extended backward and the antennae are slightly raised and divergent, enclosing an angle of about 45°.

On one occasion, a somewhat different posture was noted in a male *macrurus*. It was discovered hanging on the side of a vertical branch of a fallen log. It was early in the morning and the animal had presumably spent the night there as the temperature was 13.3° C

and it was quite lethargic and not able to move, even when examined with a hand lens (it left the log later in the day). Its position differed from that described above in that the posterior three segments of the abdomen curved sharply toward the substrate, the last one touching it. The wings were pressed more closely against the abdomen than usual although they did not overlap in the center. This may be the typical posture during the night, or it may have been a response to low temperature.

Alarm Reactions

The terminology employed here does not, of course, imply an emotion of fear in the insects but is simply a convenient descriptive term to designate certain types of behavioural reactions.

Three general types of behaviour fall under this category, (1) antenna vibration, (2) abdominal jerking, and (3) flight. The former consists of holding the slightly divergent antennae parallel to the surface on which the insect is sitting and vibrating them slightly. This appeared to be a response to loud noises and approach of large objects although it also frequently occurred immediately upon landing on a stump or log and before exploratory behaviour began. Abdominal jerking is characterized by rapid elevation of the abdomen followed by its gradual lowering to the original position. It is invoked by a tactile stimulus such as occurs when one insect comes into contact with another one. It was observed only in males of *greenei* and *atrata*. All contact resulting in abdominal jerking appeared fortuitous and there was no evidence that this constituted a threatening or warning posture. No aggressive behaviour was noted within or among these three species and the „fierce rivalry“ among males just preceding copulation mentioned by HARRINGTON (1887) has not been substantiated. It is possible that what he observed was the homosexual mountings described above or perhaps several males attempting simultaneous copulation with the same female.

Flight is such a common reaction as to not warrant further discussion except to note that less disturbance was required to cause *greenei* (of both sexes) to fly away from a site than was necessary for the other two species. Also it was the only species noted leaving the log as a result of accidental contact with other individuals.

„Pumping“ Behaviour

A type of behaviour was observed which had no apparent function and for which the causative stimuli are unknown. It will be called „pumping“. It is characterized by a slow, somewhat circular movement of the wings with a simultaneous raising and lowering of the abdomen, arching it slightly on the upward movement and straightening it on the downward one. The abdominal movement differs from abdominal jerking in being much slower. Also the latter is not accompanied by arching. Pumping was observed in both sexes of all three species.

Discussion

As shown by analysis of their sexual behaviour these three species are reproductively isolated in that the males do not mate with a female of any but their own species. This is not, however, strictly a behavioural isolating mechanism for not only is the pre-copulatory behaviour of all three species identical but males display poor sex recognition and species discrimination when in a state of extreme sexual responsiveness, as was evidenced by inter-specific homosexual mountings. Rather, reproductive isolation arises from

interspecific differences in the nature of the stimulus required to bring the males to the physiological state in which they initiate copulation. Although the initial generalized stimulus (before the female breaks through to the surface) causes a state of excitement in males of all three species, it never develops to the point where copulation takes place unless followed by the appropriate species-specific stimulus. Without the latter, animals subside into a non-responsive state. Hence, the only situation in which hybridization appears likely to occur would be if two females of different species would simultaneously emerge in close proximity, thereby stimulating males of two species. The tendency of males in a responsive state to attempt mating with any individual, regardless of sex or species, might then result in interspecific mating. However, the low rate of emergence in nature makes simultaneous emergences in close proximity by females of different species a highly improbable event. It is not known whether such matings would even then produce viable offspring. No hybrids, recognizable as such, have been observed in nature.

From the comparison of all types of behaviour in these species it is obvious that in addition to their similarities in morphology, ecology, and host preference, they are also very similar in behaviour. This further emphasizes their close phylogenetic relationship and poses additional problems in interpreting their sympatry. The apparent absence in some species of behaviour patterns which are present in others is probably due to insufficient data rather than an actual absence, particularly so when it is remembered that this was true chiefly for the less frequently observed types of behaviour. The observed difference in method of oviposition is related to mechanical requirements imposed by structural differences among the species, i. e., the relatively shorter ovipositor of *greeni* permits that species to oviposit without employing the ovipository membrane.

Because of its significance in host and mate detection, exploratory behaviour is of special interest. Only the tips of the antennae play a major role in exploration. They are continuously tapped against the substrate whereas other parts of the antennae never come in contact with it. This would strongly suggest that sensory organs located at the very end of the antennae are used in detection of hosts and mates although other sensory organs might also be involved. For example, the abdomen dipping behaviour during exploration and the sharp abdomen-bending during precopulatory behaviour place the tip of the abdomen in contact with the substrate. Accessory receptors may be located there.

Summary

The behavioural patterns of *Megarhyssa macrurus lunator*, *M. atrata lineata*, and *M. greeni greeni*, all parasitic on wood-boring larvae of *Tremex columba*, were directly observed in nature and are herein described with a presentation of their functional significance. All three species had practically identical patterns of behaviour except where differences in morphology imposed modifications of a mechanical nature.

Exploratory behaviour involves chiefly the tips of the antennae; the sensory organs located there are probably used to detect hosts although accessory receptors on the tip of the males' abdomen may also be involved in detection of females. Two stimuli seem to be involved in mate detection and selection; a generalized one which attracts males of all three species to the log and brings them to a state of sexual responsiveness, and a species-specific one which

stimulates males of only the appropriate species to initiate copulation. The latter is liberated only after the female cuts through the surface of the log.

Zusammenfassung

In freier Natur wurden bei *Megarhyssa macrurus lunator*, *M. atrata lineata* und *M. greeni*, die sich alle als Parasiten der in Holz bohrenden Larven von *Tremex columba* entwickeln, Verhaltensbeobachtungen gemacht, beschrieben und funktionell gedeutet. Alle drei Arten zeigten nahezu gleiche Verhaltensweisen, außer wenn Bauunterschiede, z. B. verschieden lange Lege- röhren mechanische Abweichungen bedingten. Dem Erkunden dienen vor allem Sinnesorgane an den Fühlerspitzen. Wahrscheinlich erspüren diese sowohl die Wirtslarve als auch den Geschlechtspartner; beim Auffinden der Weibchen dürften weitere Sinnesorgane am Hinterleibsende des Männchens beteiligt sein. Zwei Reize scheinen das Finden und die Auswahl des Geschlechtspartners zu ermöglichen: Ein allgemeiner, der die Männchen aller drei Arten zum Fundort führt, dort festhält und paarungsbereit macht, sowie ein artspezifischer, der nur die Männchen der Art, zu der das aufgefundene Weibchen gehört, zur Paarung anregt. Er tritt erst in Kraft, nachdem das Weibchen ein Loch in die Außenwand seiner Puppenwiege geschnitten hat.

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