Laboratory), and L. C. Kuitert (University of Florida) for including us in an already crowded program and personally handling our local arrangements; and the Florida Entomological Society for their gracious offer to publish these proceedings.

AGGREGATION IN MALE PARASITIC WASPS OF THE GENUS *MEGARHYSSA*[1]: I. SEXUAL DISCRIMINATION, TERGAL STROKING BEHAVIOR, AND DESCRIPTION OF ASSOCIATED ANAL STRUCTURES BEHAVIOR

R. W. MATTHEWS, J. R. MATTHEWS, AND O. CRANKSHAW
Department of Entomology
University of Georgia
Athens, GA 30602

Parasitic wasps comprise a species-rich group for which a number of casual and fragmentary observations on mating and courtship exist, but few detailed studies have been published (Matthews 1975). A singular phenomenon among them is provided by the pre-mating behavior of *Megarhyssa*, a genus of large, long-tailed ichneumon wasps parasitizing *Tremex* horntail larvae in dead trees. Males form conspicuous mixed-species aggregations on the bark of trees from which new adults are actively emerging (Fig. 1). All facing inward around a circular area of about 50 mm diameter, they jostle about and jockey for position, but show little overt aggression toward one another. When a female wasp finally chews through the bark, a conspecific male quickly mates with her, and the other males at least temporarily disperse. The most detailed previous studies of *Megarhyssa* behavior are those of Heatwole et al. (1963, 1964) and Heatwole and Davis (1965) in which most references to earlier observations may be found.

Most previous reports of *Megarhyssa* male aggregation have asserted that species identification and sex discrimination are determined as the emerging adult penetrates the outer bark surface. Several workers have noted that the waiting males often probe bark crevices with the tips of their abdomens, including penetrating the partially chewed out emergence hole. Nuttall (1973) and others have suggested that this may result in fertilization of the female within its tunnel. However, this idea has usually been discounted because of the relatively greater length of the female abdomen as compared to the male.

During the summers of 1977 and 1978 we studied male aggregation in 3 species of *Megarhyssa* found in beech-hemlock forests of an upstate New York biological station, the E.N. Huyck Preserve in Rensselaerville. Our study sites consisted of 8 isolated, dead but still standing beech trees. The maximum distance between any 2 trees was less than 100 m. Among the results described in this paper are a previously unappreciated behavior, a possible new gland, and the shedding of some new light on previous interpre-

[1]Hymenoptera: Ichneumonidae.

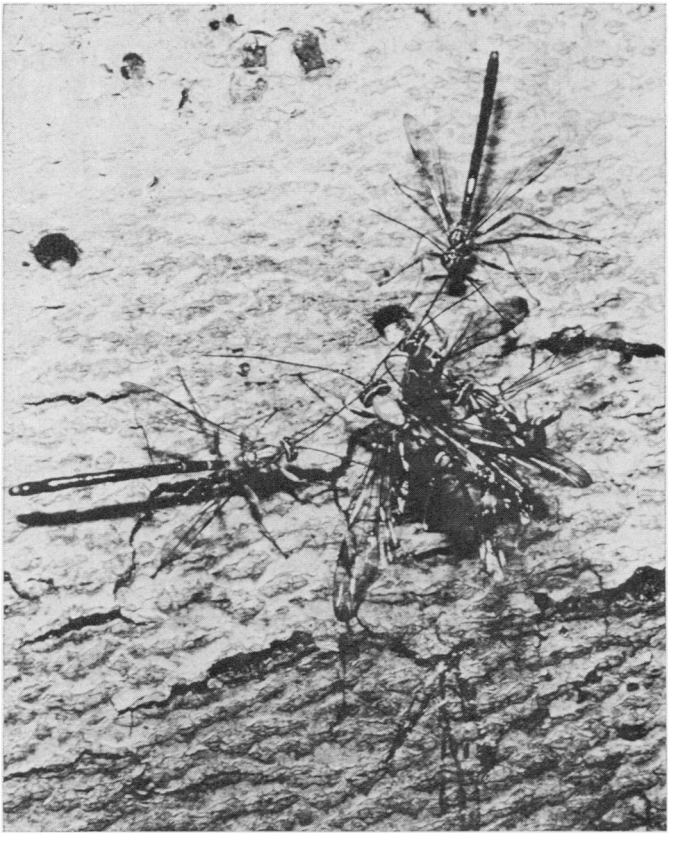

Fig. 1. Typical aggregation of several male *Megarhyssa* wasps at an emergence site on a dead beech. Two species are present and several individuals are marked with spots of paint to permit recognition.

tations of the nature and function of male aggregation in *Megarhyssa*.

In contrast to searching or patrolling males, those in aggregations are unusually tenacious; if disturbed they may fly away but normally will regroup within minutes at the same precise spot on the tree. On a longer time scale, males also show a remarkably high fidelity to particular host trees, returning to patrol them day after day. Because of this tenacity, once an aggregation is found, it is relatively easy to follow it through time and, by distinctively marking males with spots of Testor's® enamel, to monitor individual interactions. For example, in July 1977, 45 males were marked and the host trees checked at least once daily during the following month.[2] Of these, 15 were later seen again, and 64% of these recaptured individuals were found patrolling the same tree from which they had originally been recorded. This tendency to return to a particular tree was previously noted by Abbott (1934) and Heatwole and Davis (1965) and applies to both sexes.

[2]One male was sighted 24 days after being marked, a longevity which concurs with Heatwole and Davis' (1965) record of 27 days for 1 male.

The latter authors obtained an even higher fidelity to particular trees (81% and 100% for 24 and 15 males, respectively, marked in 2 consecutive years).

Within a given aggregation, the behaviors which occur seem at first quite random. In our study, these commonly included mutual antennation, antennal lashing by 1 male upon the body of another, bouts of wing vibration, abdomen flexing, probing crevices with the abdominal tip, and head butting, all of which confirmed the previous observations of other researchers. Both before and after the emerging adult chewed through the bark, some males exhibited a very distinctive behavior which we called "tergal stroking". Males performing this behavior adopt a stereotyped posture (Fig. 2), with the abdomen thrust well forward between the legs until its dorsal surface touches the substrate, its tip lying between the tips of the antennae. Only the dorsum of the ultimate abdominal segment touches the bark; the genitalia at the tip of the abdomen do not contact the substrate (contrary to observations of similar behavior mentioned by Heatwole et al. 1963), nor are the claspers extended. In this position, the male wasp repeatedly thrusts its abdomen forward in short, anteriorly-directed strokes along the substrate.

On males of all 3 species of *Megarhyssa*, there is a large membranous and partially eversible sac (Fig. 3, inset) opening at the apex of the last (8th) tergite, adjacent to the base of the genital capsule. The occurrence of this possible anal gland does not seem to have been reported previously. On its dorsal surface, scanning electron microscopy reveals the presence of a dense tuft of setae resembling an applicator brush (Fig. 3). Although close examination of this anal sac after treatment with 10% potassium hydroxide solution failed to reveal a cuticle-lined glandular structure, it is possible that tergal marking materials are derived from cells of the hind gut, which

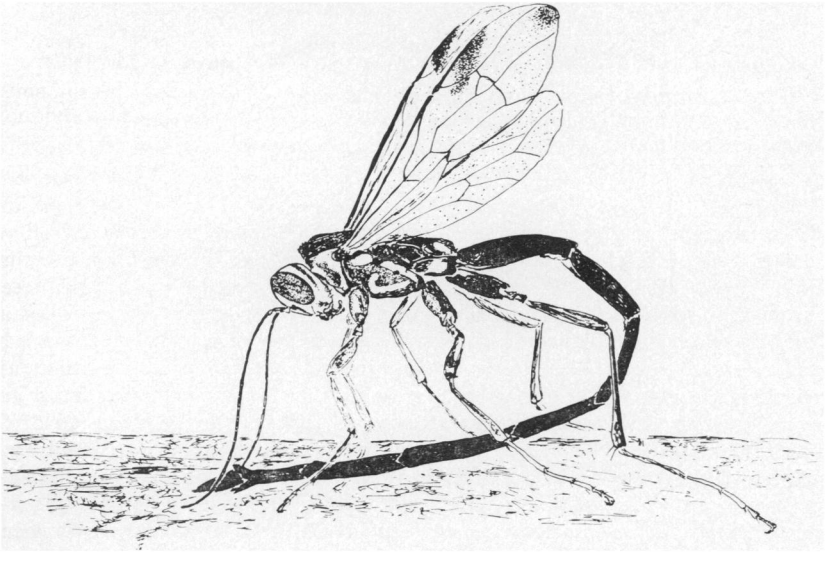

Fig. 2. Sketch of a male *Megarhyssa macrurus* (L.) performing the tergal marking behavior. (Drawing by Joan W. Krispyn)

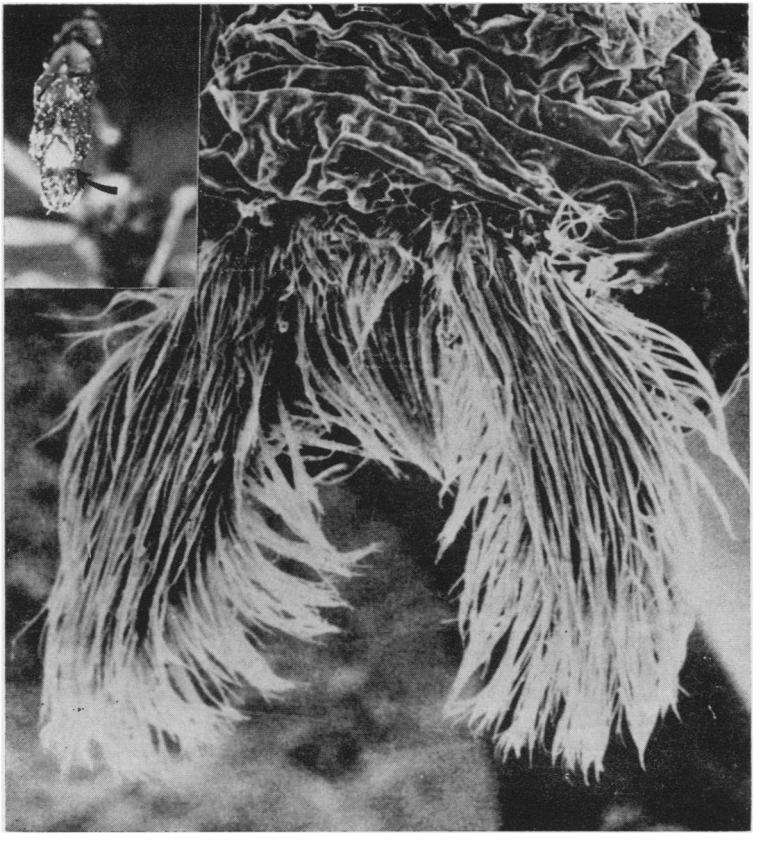

Fig. 3. Scanning electron micrograph of partially everted "anal gland" of *Megarhyssa greenei* Viereck showing the dense tufts of setae which form a brush-like applicator (dorsal aspect, 200x). Abdomen of a male *Megarhyssa macrurus* showing the large membranous area on the posterior dorsal surface.

also terminates at this point. Hand-held males will readily excrete a droplet or 2 of fluid, possibly liquid waste products, from this opening. No odor is discernable from the male anal area. Although a possible protective odor has been noted for *Megarhyssa* (Townes 1939), our observations indicate that this odor appears to emanate from glands in the head. Whatever further study clarifies about the histology of this possible gland, analysis of films of individuals performing tergal stroking make it quite apparent that the setal brush actively strokes the substrate. A closely similar behavior is that which Heatwole et al. (1963) term "dipping," in which males bend the abdominal tip downwards and drag it along the substrate for several centimeters, in an action reminiscent of trail-laying in ants. We have also observed this behavior on a few occasions, but it differs from tergal stroking in that the abdomen is arched so that the tip of the genitalia contact the bark. Also dipping tends to be performed while walking over the bark, rather than at aggregation sites.

In 1978, 16 aggregations involving marked individuals were studied for extensive time periods. Thirteen of these aggregations were of mixed species composition, the other 3 consisting of a single species. In each case, 1 or 2 individuals performed the majority of the tergal stroking bouts and crevice insertions. When the aggregation was artificially dispersed, those returning appeared to maintain the same relative status, and these "dominants" resumed their stroking bout with the same frequency as they had shown previously. Such "dominance" may be simply a reflection of internal milieu. It may also be related in some manner to conspecificity with the emerging adult, although in 3 of the 13 mixed species aggregations the emergent was of a different species from the "dominant" stroking/inserting male.

Tergal stroking does not appear to be related to the sex of the emerging individual. Males in aggregations are much less discriminating in this regard than has previously been thought. It appears that little sex discrimination is taking place at all at the moment the new adult first penetrates the bark, as previous workers have asserted (Heatwole et al. 1964). Even when males subsequently emerged, tergal stroking and insertion proceeded, unabated, up to the time of actual mounting attempts. On several occasions, as the new male emerged it was mounted almost immediately, and repeated copulatory attempts were made by the aggregated males.

By affixing small screen cages over emergence sites where males were congregating, we were able to record the sex and species of the emerging adults for 35 aggregations. Of these, 12 yielded males and 23 produced females. Males aggregated with equal intensity at sites from which either sex emerged, and no behavioral differences correlated with the future emergent's sex were demonstrable. Although Heatwole et al. (1964) observed 31 aggregations no data are recorded for the outcome of 20 of these except that 3 yielded wood-boring insects other than *Megarhyssa*. The remaining 11 all yielded females.

The function(s) of the anal gland and of tergal stroking are unknown. Were a clear-cut sexual bias evident, classic possible roles might include aphrodisiac effects or other involvement in female receptivity alteration, territorial marking, or an olfactory "display" function. We suspect that it may be related instead to the behavior in which males repeatedly attempt to insert their abdomens into bark crevices and emergence holes. Frequently they penetrated the emergence hole, thrusting their abdomen deeply (often all the way to the thorax) and snugly along the side of the emerging adult. The positional relationship of the inserting male to the emerging adult is such that the setal brush rubs along the body of the emerging adult. It seems unlikely that such behavior is attempted copulation, given the frequency with which such insertion behavior occurs at sites from which males subsequently emerge.

If the rate at which receptive females are encountered determines a male's overall reproductive success, selection should favor extreme male mobility or the guarding of areas where receptive females are most likely to be found (Parker 1970, 1973). It should also favor any other process which increases the rate at which females are encountered. Tergal stroking and insertion might both contribute to such an increase. For example, the propensity to perform tergal stroking at all emergence sites irrespective of sex or species of the emerging individual may serve to reinforce the male's tendency to return to particular trees. This would be adaptive from the

male's standpoint, since if *Megarhyssa* are emerging from the tree, there is a strong likelihood that more adults will issue from the same tree in subsequent days and that at least some of them will be conspecific females.

Concurrently, time invested with a slowly emerging male might cost a female emergence to be missed on the other side of the tree. Selection would be expected to favor any male behavior which minimized the time invested in unfruitful aggregations, as well as behaviors increasing the rate of successful encounters. Pre-mating discrimination, although potentially advantageous, apparently does not occur. If the insertion behavior hastens the emergence of the new adult which is being stroked, it would be advantageous for a male to perform this behavior with any emerging wasp regardless of sex or species. It would decrease the length of time he would need to invest at a particular emergence site. Further study of the sexual behavior of male *Megarhyssa* wasps will clearly be revealing in the context of sexual aggregation and discrimination.

Acknowledgements

This research was supported by grants from the Edmund Niles Huyck Preserve, Rensselaerville, New York. Our special appreciation is extended to Joan Krispyn who executed the ink drawing and to Karl Scott who took the SEM photograph. Kathy Jablonski, Wayne Gardener and Kenneth Suarez, members of an EARTHWATCH team assigned to the E. N. Huyck Preserve, were enthusiastic and helpful assistants during 1977.

Literature Cited

Abbott, C. E. 1934. Notes on *Megarhyssa lunator*. Psyche 41:238-40.

Heatwole, H., D. M. Davis, and A. M. Wenner. 1963. The behavior of *Megarhyssa*, a genus of parasitic hymenopterans (Ichneumonidae: Ephialtinae). Zeit. Tierpsychol. 19:652-64.

———, ———, and ———. 1964. Detection of mates and hosts by parasitic insects of the genus *Megarhyssa* (Hymenoptera: Ichneumonidae). Amer. Midl. Nat. 71(2):374-81.

———, and ———. 1965. Ecology of three sympatric species of parasitic insects of the genus *Megarhyssa* (Hymenoptera: Ichneumonidae). Ecology 46:140-50.

Matthews, R. W. 1975. Courtship in parasitic wasps. Pp. 66-86 *In* P.W. Price, ed., Evolutionary Strategies of Parasitic Insects and Mites, Plenum Publ. Co., N.Y.

Nuttall, M. J. 1973. Pre-emergence fertilization of *Megarhyssa nortoni* (Hymenoptera: Ichneumonidae). N. Z. Ent. 5:112-7.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 46:528-68.

———. 1973. Courtship persistence and female-guarding as a male time investment strategy. Behaviour 48:157-82.

Townes, H. K. 1939. Protective odors among the Ichneumonidae (Hymenoptera). Bull. Brooklyn Ent. Soc. 34:29-30.