Behav Ecol Sociobiol (1981) 9:1–7

Behavioral Ecology and Sociobiology

Sexual Behavior Among Parasitic *Megarhyssa* Wasps (Hymenoptera: Ichneumonidae)

Owen S. Crankshaw* and Robert W. Matthews

Department of Entomology, University of Georgia, Athens, Georgia 30602, USA

Received July 28, 1980 / Accepted April 28, 1981

Summary. Male wasps of three sympatric species of Nearctic *Megarhyssa* (Hymenoptera: Ichneumonidae) typically form mixed-species (61.7%) aggregations composed of up to 28 males over sites of female emergence. Observations of 107 aggregations over two seasons in New York state revealed two male mating strategies: postemergence copulation on the tree surface and preemergence insemination accomplished by male abdominal insertion into the female emergence hole. Insertions by one or more males (as many as ten consecutively but not more than two simultaneously) occurred at 88% of the aggregations, with each inserting for an average of 24.8 min. Insemination as a result of preemergence insertion had a success rate of 83% while postemergence copulation attempts were successful 30% of the time (average duration 61.9 s). Individual male reproductive success was very low and not correlated with size, arrival order at emergence sites, or tenacity at the site. Males frequently aggregated at sites of male emergences as well as those of nonconspecifics, though conspecifics to the emerger ultimately played the major role at aggregations. Male-male aggression in aggregations was not apparent, though jostling occurred during the insertion period and during postemergence copulation attempts.

Introduction

Recently, analytical work on mating strategies of insects has intensified in an effort to test current sexual selection theory (Parker 1978; Thornhill 1976). A review of the mating behavior of bees and aculeate wasps (Alcock et al. 1978) revealed that the Hymenoptera are suitable for examination of the mating strategies of males in relation to the temporal availability of females and/or the spatial distribution of resources.

Megarhyssa is a genus of ichneumonid wasps that includes some of the largest members of the family. The sexual behavior of three sympatric species of these parasitic wasps has some unusual features. Males form conspicuous mixed-species aggregations on the surface of trees at sites where adults are emerging (Matthews et al. 1979). Time investment by males at emergence sites is quite high prior to surface penetration by the emerger. Females apparently mate only once. Thus, selection pressure would seem to favor males that successfully copulate at the earliest possible opportunity with the females, perhaps even prior to emergence. If receptive females or their emergence sites are economically monopolizable in space and time, males would be predicted to adopt a 'female defence polygyny' strategy (Emlen and Oring 1977). One behavior favored in such a system might be early detection of new emergence sites.

The present study describes the composition and characteristics of *Megarhyssa* male aggregations studied over two seasons. Individual male behaviors occurring at aggregations are analyzed in terms of male time investment.

Materials and Methods

General Biology. The genus *Megarhyssa* is represented by three sympatric species in the northeastern United States: *M. atrata*, *M. macrurus*, and *M. greenei* (Townes and Townes 1960). These long-tailed wasps all parasitize the same host, *Tremex columba* (Hymenoptera: Siricidae), wood-boring horntail larvae in deciduous trees. Adult *Megarhyssa* are 2.2–5.1 cm in length, depending upon sex and species, with males generally smaller than females. The egg is laid on or near the *Tremex* larva; the larva consumes its host and emerges the following year as an adult (Stillwell 1967). Males generally emerge prior to females, spending nearly their entire adult life waiting for other adults to emerge. All three species

* Current address and that for offprint requests: Pesticide Research Center, Michigan State University, East Lansing, Michigan 48824, USA

0340-5443/81/0009/0001/$01.40

overlap in seasonal occurrence (Heatwole and Davis 1965) and a majority of aggregations are interspecific. *Megarhyssa* have been the subject of behavioral notes since at least 1882 (Harrington 1882; Lintner 1883). The most recent studies are those of Heatwole et al. (1963, 1964, 1965), which described the general behavior, host and mate detection, and ecology. Matthews et al. (1979) have reported on male aggregations and described the gross morphology of a brushlike anal structure on males. The possibility that sympatric speciation resulted in the three species of *Megarhyssa*, all of whom have virtually identical life histories, has been explored by Gibbons (1979).

Procedures. Field studies were conducted at the Edmund Niles Huyck Preserve in Rensselarerville, New York, from June 5 to August 30, 1978 and May 18 to August 6, 1979. Observations were made daily from 10 a.m. to 4 p.m., temperature permitting (wasps were inactive below 12 °C). At the study sites, wasp activity was confined to horntail-infested beech trees (*Fagus grandifolia*), which were sometimes heavily damaged by pileated woodpeckers.

As wasps were encountered, they were marked on the thorax and/or abdomen with Testors paint for individual identification. Using a five-color system, 347 males were marked in 1979; 172 males and 75 females were marked in 1978. Wasps were usually marked at the beginning and end of the day to minimize disruption of their activities.

Females into whose emergence holes males had inserted their abdomens were collected prior to external mating and chilled. Subsequently, their spermathecae were dissected and viewed under a phase contrast microscope to check for the presence of sperm.

In 1978 and 1979, five trees were watched closely using a trapline technique. The trees were located in two study areas with a maximum intertree distance within each area of 130 m. Locations of activities of all marked wasps were noted. When observations of aggregations had to be interrupted but the emerger sex and species identification was desired, conical screen traps were affixed to the bark surface over the emergence site.

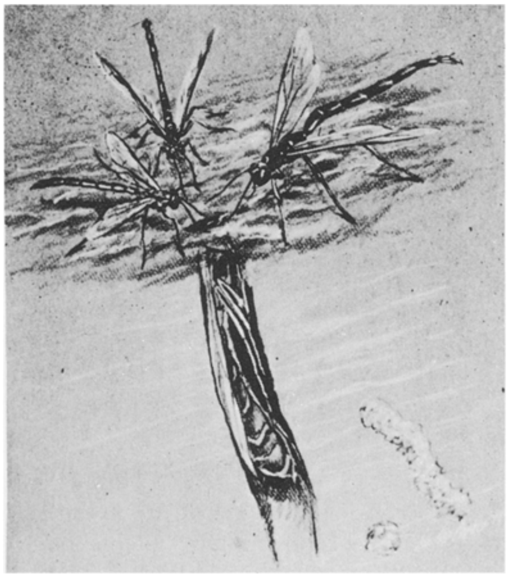

Fig. 1. Diagrammatic representation of males gathered over site of female emergence

Table 1. The number of male aggregations of various species compositions for three sympatric *Megarhyssa* species observed in 1978 and 1979

Aggregation composition	No. male aggregations observed
M. greenei	29
M. macrurus	1
M. atrata	11
greenei + macrurus	28
greenei + atrata	10
macrurus + atrata	5
greenei + macrurus + atrata	23

Results

Aggregations

Males patrol from tree to tree only during daylight hours, so they were seen on only a few host trees within the study area. Home range was not determined, but the maximum distance a marked male was recorded to move was 200 m. Upon approaching a host tree, a searching male may immediately land on the bark or he may slowly circle the tree with his body axis positioned roughly perpendicular to the tree surface and his outstretched antennae touching the surface. Once landed he may remain in a particular area for intense searching and antennation; alternatively he may undertake apparently random searching on the tree surface or resume flying around the tree. Upon discovery of a prospective emergence site, the male antennated it vigorously, apparently pinpointing the location of an emergence. He may then remain still, antennate more, move around or begin flexing his abdomen. From this point, either the emerger's chewing noises or the initial male's presence may serve as an attraction to other searching males that begin landing at the site and antennating; this resulted in the formation of an aggregation (Fig. 1). Aggregating males often bent their abdomens ventrally to rest the abdominal tip on the bark surface (tipping), or they curled the abdomen under them such that the last two tergites contacted the bark surface (tergal stroking).

Aggregations were characteristically composed of more than one species (Table 1). Aggregations involving *M. macrurus* were more likely to be interspecific, due in part to its midseason occurrence. *M. greenei* was most likely to have conspecific aggregations (*greenei* emergences extend the latest in the season). Overall, 61.7% of observed aggregations were conspecific. Compositions of 80 aggregations in relation to the sex and species of the emerger is given in Table 2.

Prior to surface penetration by the emerging individual, the behavior of aggregants was characterized by intense antennation, periods of motionlessness, abdominal tipping, and tergal stroking. When the

Table 2. Species compositions of male *Megarhyssa* aggregations at sites of known emerger sex and species. Figures represent the number of aggregations observed with a known emerger that had the given species composition

Emerger	Species of males composing aggregations						Totals
	atrata only	*atrata* + *macrurus*	*atrata* + *greenei*	All three species		Males absent	
atrata female	8	2	1	2		0	13
atrata male	0	0	0	1		0	1
	macrurus only	*macrurus* + *atrata*	*macrurus* + *greenei*	All three species	*atrata* only	Males absent	
macrurus female	0	2	7	1	0	2	12
macrurus male	0	1	3	0	3	0	7
	greenei only	*greenei* + *atrata*	*greenei* + *macrurus*	All three species	*atrata* only	Males absent	
greenei female	11	1	7	6	0	0	25
greenei male	12	3	3	2	1	1	22

emerger was close to penetrating the surface, the intensity of male activity increased and included jostling and an intense effort to keep the abdomen tipped at the site where the hole was to appear. The ratio of males conspecific with the emerger to nonconspecifics usually increased at this point, from a ratio of 2:1 soon after aggregation formation to a ratio of 3.8:1 at the point of the surface break by the emerger. This occurred both by an increase in conspecifics arriving and by the exodus of nonconspecifics.

As the emergence hole appeared, activity proceeded regardless of the sex of the emerger (Matthews et al. 1979). However, when the emerger was a male, usually fewer aggregants were present (average of 5.5 per aggregation) than when the emerger was a female (average of 6.6 per aggregation), and activity was less intense. For the 5–20 min between surface penetration and emergence, males exhibited rather stereotyped behavior. Those males that were 'tipped' immediately attempted to insert their abdominal tips into the hole. Insertions occurred at 88% of the aggregations, with as many as eight males partially inserting their abdomens into the incipient emergence hole simultaneously.

Apparently the emerger can still chew somewhat; the hole slowly enlarged despite the blockage by male abdomens. The maximum number of males was present at the aggregation at this point (Fig. 2). Sometimes the inserting males belonged to all three species, but conspecifics were in the majority at all times (Fig. 3). Males inserted at a majority of the emergences of conspecifics of both sexes and at a minority of the emergences of nonconspecifics (Table 3). Indeed, males were aggregated correctly over conspecif-

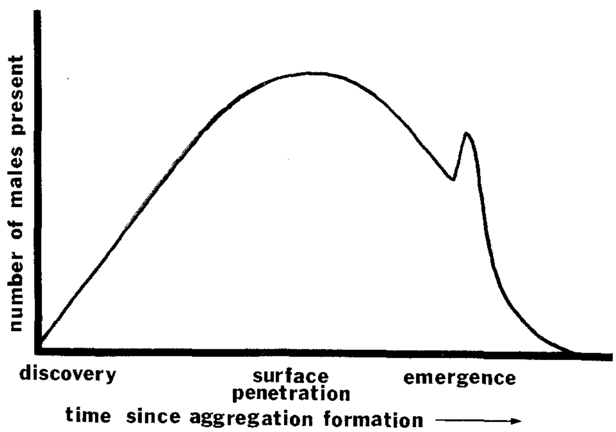

Fig. 2. Relative number of males of all species present in an aggregation at selected stages during the emergence of a female *Megarhyssa* wasp

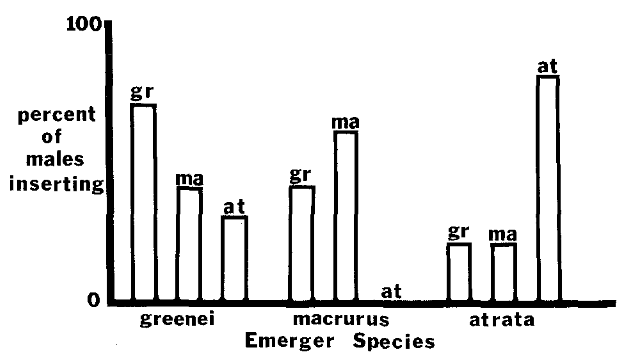

Fig. 3. The relation between the species of the emerging adult and the percentage of males belonging to each species of *Megarhyssa* present in an aggregation that were observed to insert their abdomens. *gr greenei; ma macrurus; at atrata*

Table 3. Aggregation composition and species of emerger related to occurrence of male insertions by all three *Megarhyssa* species at 42 selected aggregations, showing the degree of specificity of male insertions

Species inserting	Insertion occurrence	Aggregation composition and species emerging									
		greenei + macrurus		*greenei + atrata*		*macrurus + atrata*		*greenei + macrurus + atrata*			
		greenei	*macrurus*	*greenei*	*atrata*	*macrurus*	*atrata*	*greenei*	*macrurus*	*atrata*
greenei	Yes	9	3	3	0	–	–	6	1	0
	No	1	4	2	1	–	–	2	2	3
macrurus	Yes	4	5	–	–	3	0	1	3	0
	No	6	2	–	–	0	2	7	0	3
atrata	Yes	–	–	1	1	2	2	2	2	2
	No	–	–	4	0	1	0	6	1	1

ic females 44% of the time, which suggests a level of discrimination which, while not perfect, is better than that expected by chance alone (17%, since emergers fall into six categories by species and sex). Males excluded from inserting jostled at the perimeter of the aggregation, antennated the hole and flexed their abdomens toward the hole. Conspecifics present at the time of surface penetration were quite tenacious; only rarely did they leave the site. However, nonconspecifics tended to leave singly from this point on, changing the ratio of conspecifics to nonconspecifics to 4.3:1 by the time of the actual emergence from the hole.

As the hole enlarged, males were able to push more than one or two segments into the hole, eventually getting all of their abdomen and part of the thorax inserted. A male remained inserted (defined as the time from initial tip insertion to complete withdrawal) for 2–410 min ($n=59$, $\bar{x}=24.78$). Only 1 or 2 males were able to insert fully at the same time; however, 1–10 males may insert consecutively in an emergence hole over the course of the emergence ($\bar{x}=2.4$). The average size of first inserters did not differ significantly from the average size of all male aggregants, nor was there a correlation between order of arrival at the site and order of insertion. In 90% of the observed insertions ($n=187$), the male left the aggregation following withdrawal after having inserted fully. Less than 30% of those males were observed to return by the time of emergence. Often males stood nearby while a female emerged (after having inserted upon her) without taking further part in mating attempts. If the emerger was a male, few aggregants remained and they displayed little interest in the emerger. If it was a female, males became very active and attempted to copulate with her, even before she was fully emerged.

Upon emerging, the female generally began walking up the tree followed by males who attempted to mount her. Pursued females either attempted to brush off the males or remained more or less quiescent until one male successfully coupled. Males left on the tree following a female's exit and departure did not attempt to follow her, but instead vigorously antennated the emergence hole, and/or patrolled the immediate area for up to 10 min more before dispersing. Occasionally a male that had been in contact with the newly emerged female or one that has inserted upon her was attractive to other males present who then attempted homosexual mountings. Occasionally some males also continued to insert into the empty emergence hole for 1–2 min. These observations suggest the existence of a female sex pheromone.

Preemergence Mating

Attempts by aggregated males to insert their abdomens was a major time-consuming behavior during the aggregation. Of males that spent 30 or more min at an aggregation ($n=21$), an average of 29.5% of their time was occupied with actual insertion, and another 30.5% of their time involved tergal stroking and tipping, behavioural precursors to insertion.

Possible functions of insertion might include female receptivity alteration, female monopolization through the exclusion of other males, determination of emerger sex or species and preemergence insemination. Observations on aggregations showed that sex and species determination occur primarily following surface penetration, and perhaps to a limited degree prior to it. Thus, it seemed unlikely that insertion behavior evolved solely for this purpose. The exclusion of other males did occur, especially when one inserter remained inserted for prolonged periods; however, female emergence was prohibited until the inserted male withdrew, and other males often inserted immediately at that point. Postemergence mating by the major inserter was rare; on only two occasions was the major inserter in the aggregation the male that mated following emergence. Therefore,

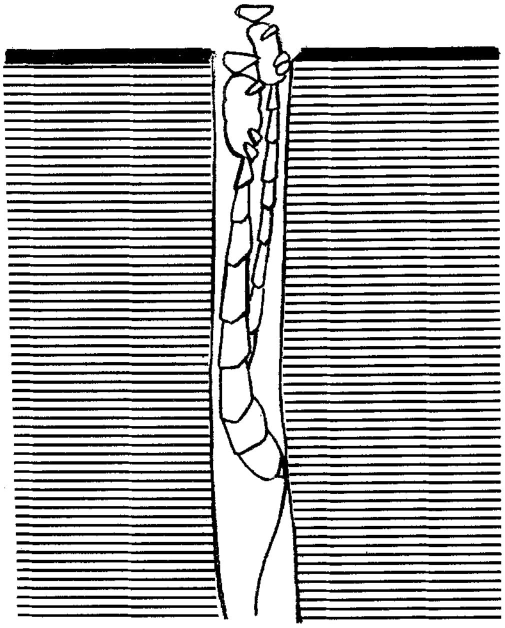

Fig. 4. Diagrammatic representation of an insertion mating in *Megarhyssa*

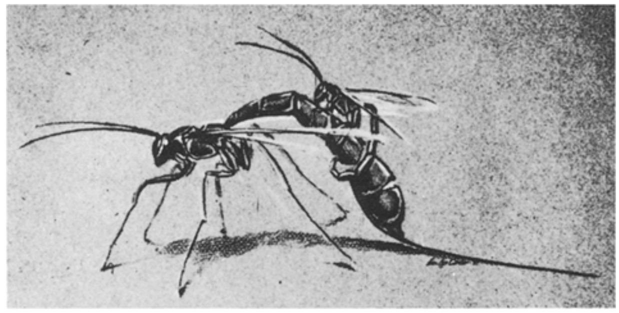

Fig. 5. Posture assumed in a typical postemergence mating of *Megarhyssa* showing how the male curves his abdomen to achieve coupling

mate selection by a female for postemergence mating based on male insertion probably does not occur.

The possibility of preemergence insemination has been suggested previously (Gade 1884; Harrington 1887; Champlain 1921; Nuttall 1973). However, Heatwole et al. (1963) discounted the idea due to the much greater length of the female in comparison to the male. We examined the possibility that preemergence insemination might be occurring from three standpoints: (1) presence of sperm in the female spermatheca, (2) reproductive lengths of males and females, and (3) physical alignment of the male and female genitalia and abdomens.

Spermathecae of six females were examined for the presence of sperm subsequent to male insertion. Five of these proved to be inseminated.

Determination of the reproductive length of 146 males and 66 females were made. Male reproductive length (measured from the metathorax to the tip of the genitalia) was 81% of total body length while female reproductive length (measured from the head to the genital opening) comprised 71% of the total body length exclusive of the ovipositor. Physical alignment of male and female genitalia was considered possible since the female's external genital opening is situated three segments anterior to the caudal end, while the male's genitalia are on the terminal segment. When the male was fully inserted (up to the metathorax) in the emergence hole, the average inserted length (=reproductive length) was greater than the average distance from the female's head to her genital opening for that particular species (Fig. 4). This does not take into account the male's ability to stretch his abdomen and the female's ability to contract; both sexes can alter their abdomen length considerably. Thus, an average female's genital opening was physically accessible to most conspecific males for preemergence insemination.

In certain respects, preemergence mating would appear to be more straightforward and easily accomplished than postemergence mating, for the female genital opening is oriented anteriorly while the male genitalia project posteriorly. When in copula prior to emergence, the male needs simply to insert his abdomen straight down the hole and directly into the female's genital opening (Fig. 4). However, when copulation is performed after the female emergence, the male must mount her abdomen and curl his abdomen 360° to properly connect with her genitalia (Fig. 5).

Postemergence Mating

As mentioned previously, following female emergence coupling may occur on the tree surface. Coupling followed 31% of aggregations where a female emerged undisturbed ($n=24$). Of the postemergence mating attempts, 69% occurred at interspecific aggregations and 31% occurred at aggregations involving only individuals conspecific to the emerger. Of the 15 aggregations where mating was attempted, the female appeared receptive to male attempts only seven times. When the female was not receptive, males are brushed off with the hind legs before copulation can occur. When the male was able to remain on the female and insert his genitalia, this behavior was accompanied by a rhythmic side-to-side rocking motion, with the actual coupling lasting for 6–170 s ($n=7$, $\bar{x}=61.9$). Four interspecific postemergence mating attempts were observed (three of female *greenei* and male *macrurus*, and one of female *macrurus* and male *atrata*); in two cases, the wasps appeared to be in *copula*. It is not known whether cross-fertilization can occur, but we have found occasional individuals which appeared to have characteristics of two species.

Discussion

Megarhyssa males spend a great deal of time at aggregations over emergence site of 'wrong' species and sex. They appear to have only limited ability to distinguish conspecific females; the frequency of insertions on nonconspecifics and on other males is high. Yet within a given aggregation males do seem capable of limited discrimination, for conspecifics to the emerger play the major role, and insertions occur less frequently on males than on females. Males spend a large portion of time waiting for the emerger to pierce the bark surface, at which time they immediately attempt to insert. The endeavor to insert as soon as possible often seems to override selectivity.

The data presented here indicate that females seem to have a greater probability of being inseminated by males through insertion mating than by postemergence mating. Whether the preemergent female will allow more than one male to enter her genital opening during insertion is unknown. However, if females are strictly monandrous, which would be consistent with most parasitic Hymenoptera (Matthews 1975), and receptive at the time of bark surface penetration, then one would predict that natural selection would favor males who were the first to fully insert on her. Though overt aggression was not apparent in male aggregations, intense male-male competition appeared to be occurring throughout the insertion period.

No hierarchy system was detected among the aggregating males, based either on size or order of arrival. Presumably a male that arrived just prior to the surface penetration would have the same chance to insert as would the first male at the aggregation, since males were unable to monopolize sites of female emergence. Since insemination may occur quickly following surface penetration, male activity and competition should be most intense at the point of surface penetration, and this was the case. The observed decline of male activity at aggregations following the first insertion would be consistent with having females that mate only once, for it would be advantageous for males to be able to recognize when a female was inseminated so that they may search out new emergence sites. Thus, an optimal male strategy in *Megarhyssa* would be to be at the right place at the right time, i.e., when the emerger first penetrates the bark surface. If preemergence insemination is impossible due to size, competition, or late arrival time, then an attempt at postemergence coupling should be made. In this sense aggregating males may be said to display a conditional strategy (Dawkins 1980).

The fact that females apparently mate but once and are predictably receptive, even before they fully chew through the bark, suggests that some type of female defense polygyny (as defined by Emlen and Oring 1977) ought to have evolved in *Megarhyssa*. However, the dispersed, unpredictable, and asynchronous nature of female emergences coupled with the inability of males to discriminate the sex and species reliably of the emerger (at least during the early stages of aggregation) seem to have mitigated against such a mating system, probably because virgin *Megarhyssa* females are simply not economically monopolizable. Indeed, defence of an area prior to emergence would have proved futile in 83% of emergences (percentage of male and nonconspecific emergences). If a male waited to take up defense until identification of the emerger was certain, the potential territory would already have several males in it creating intolerably high costs to obtain exclusive use of it.

Defense of a 'microterritory' consisting of only the actual emergence hole may be occurring, being the outcome of male competition for the privilege of insertion. No more than two males were ever able to insert fully on an emerging female, and the prolonged duration of insertions observed could be considered as a form of female monopolization. In this restricted sense, males may indeed be practicing a form of female defense polygyny.

Acknowledgements. This work was supported in part by the Edmund Niles Huyck Preserve, Inc., in Rensselaerville, New York, and by the Michael Award from the College of Arts and Sciences, University of Georgia. Kip Carter provided the drawings. Many thanks to Lynne Crankshaw and Janice Matthews for field and technical assistance. Comments made by Drs. A.O. Lea and C.W. Berisford of the University of Georgia and an anonymous review considerably improved the manuscript. This study is part of a thesis submitted in conformity with the requirements of the M.S. degree at the University of Georgia by the senior author.

References

Alcock J, Barrows EM, Gordh G, Hubbard LJ, Kirkendall L, Pyle DW, Ponder TL, Zalom FG (1978) The ecology and evolution of male reproductive behaviour in the bees and wasps. Zool J Linn Soc 64:293–326

Champlain AB (1921) The curious mating habit of *Megarhyssa atrata* (Fab.) (Hymen.: Ichneumonoidea). Entomol News 32:241

Dawkins R (1980) Good strategy or evolutionarily stable strategy? In: Barlow GW, Silverberg J (eds) Sociobiology: Beyond Nature/Nurture? Westview Press. Boulder, CO, pp 331–367

Emlen ST, Oring CW (1977) Ecology, sexual selection and the evolution of mating systems. Science 198:215–223

Gade G (1834) Bull Brooklyn Entomol Soc 7:103–104

Gibbons JRH (1979) A model for sympatric speciation in *Megarhyssa* (Hymenoptera: Ichneumonidae): competitive speciation. Am Nat 114:719–741

Harrington WH (1882) Long-stings. Can Entomol 14:81–84
Harrington WH (1887) The nuptials of *Thalessa*. Can Entomol 19:206–209
Heatwole H, Davis DM, Wenner AM (1963) The behavior of *Megarhyssa*, a genus of parasitic hymenopterans (Ichneumonidae: Ephialtinae). Z Tierpsychol 19:652–664
Heatwole H, Davis DM, Wenner AM (1964) Detection of mates and hosts by parasitic insects of the genus *Megarhyssa* (Hymenoptera: Ichneumonidae). Am Midl Nat 71:374–381
Heatwole H, Davis DM (1965) Ecology of three sympatric species of parasitic insects of the genus *Megarhyssa* (Hymenoptera: Ichneumonidae). Ecology 46:140–150
Lintner JA (1883) The black long sting. Country Gentleman 48:561
Matthews RW (1975) Courtship in parasitic wasps. In: Price PW (ed) Evolutionary strategies of parasitic insects and mites. Plenum Press, New York, pp 66–86
Matthews RW, Matthews JR, Crankshaw OS (1979) Aggregation in male parasitic wasps of the genus *Megarhyssa:* I. Sexual discrimination, tergal stroking behavior, and description of associated anal structures behavior. Fl Entomol 62:3–8
Nuttall MJ (1973) Pre-emergence fertilisation of *Megarhyssa nortoni nortoni* (Hymenoptera: Ichneumonidae). NZ Entomol 5:112–117
Parker GA (1978) Sexual selection and sexual conflict. In: Blum MS, Blum NA (eds) Sexual selection and reproductive competition in insects. Academic Press, New York, pp 123–166
Stillwell MA (1967) The pigeon tremex, *Tremex columba* (Hymenoptera: Siricidae), in New Brunswick. Can Entomol 99:685–689
Thornhill R (1976) Sexual selection and paternal investment in insects. Am Nat 110:153–163
Townes HK, Townes M (1960) Ichneumon-flies of American north of Mexico: 2. Subfamilies Ephialtinae, Xoridinae, Acaenitinae. US Natl Mus Bull 216 (part 2)