Mating Behaviour of the Braconid Wasp, *Apanteles glomeratus* L. (Hymenoptera : Braconidae) in the Field¹

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Mating behaviour of *Apanteles glomeratus* in a cabbage field was observed. In general, males initially emerged from the cocoon cluster. Males stayed on or near the cluster exhibiting wing vibration and antennal movement: More than half of the males was observed near the cluster for at least 5 minutes. The evidence suggested that a sex pheromone existed in cocoons and attracted males of the same- and from the other- cocoon cluster. The cocoon clusters left in the field for more than 5 days and after washing with ether lost their attractive ability for males. The active space of pheromone was about 10 cm in radius. Females after emergence walked several cm from the cluster and stood still where they were encountered by searching males. Mating took place within 5 min. after the emergence of the female. Females after mating flew away, and males again began searching. Ratio of sib-matings in *A. glomeratus* was about 60%. Inbreeding was considered to be natural in this species.

INTRODUCTION

Mating behaviour of *Apanteles glomeratus* L. under laboratory conditions has been investigated by some authors, and the existence of a female sex pheromone has been reported (OBARA and KITANO, 1974; KITANO, 1975; TAGAWA, 1977).

KITANO (1976) suggested that the difference in the behaviour of the sexes after their emergence in the field might be important in decreasing the chances of inbreeding.

However, there remains some problems concerning the mating behaviour of this species in the field: How long does the pheromone activity remain? How wide is the active space of the pheromone? When and where does mating take place? The present work was undertaken to answer these questions by continuously observing the behaviour of the wasps after their emergence in the field.

MATERIALS AND METHODS

The present work was carried out in a cabbage field on the campus of the Kyoto University in Kyoto, from May to June in 1979. *A. glomeratus* were obtained from parasitized host larvae, *Pieris rapae crucivora*.

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Cocoon clusters immediately before emergence were fixed on the upper surface of the cabbage leaves with Scotch double-stick tape. At first, ten clusters of cocoons were set on the leaves to supply enough wasps to observe. After the initial placement of cocoons, a new cluster was added to a leaf every day. Each of the clusters was set 10 to 20 cm apart. Our observations on the behaviour of the wasps were carried out from 9 A.M. to 2 P.M. every day.

The movement of the wasps was traced until the time of their departure. The sites where the males first exhibited wing vibration and the sites where copulation took place were recorded. The time required for successful copulation after female emergence and the duration of time males remained near the cocoons after their emergence was also recorded.

Finally, the cocoon clusters, immediately after the emergence of the wasps, were washed by ether to remove the pheromone adherent to them (KITANO, 1975) and fixed on the cabbage leaves to examine the attractiveness of the clusters.

RESULTS

A behaviour pattern of *A. glomeratus* is shown in Fig. 1. In all our observations, the initial emergence from cocoons in a cluster was the male. All males exhibited wing vibrating behaviour on the cluster immediately after emergence. They also intensely moved around the cluster with their antennae held forward and slightly moving them. The area where the males showed this intense searching behaviour seemed to be restricted within several cm from the cluster.

An example recorded on a sunny calm day is given in Fig. 2. It shows the sites where the males from other-cocoon clusters began wing vibration and the sites where successful copulation took place. On this day, ten males exhibited wing vibration within 5 cm of the newly placed cocoon cluster and four exhibited wing vibration on the empty cocoon clusters placed on the day before. Copulation also took place near the new cluster.

From the data of our observations, it was revealed that 88% of males from other-

Fig. 1. Behaviour pattern of *A. glomeratus* after emergence on cabbage leaves. The cabbage plant is sketched by overlooking. (●, newly set cocoon cluster. ○, empty cocoon cluster.) 9 : 10-9 : 20, 4th June.

Fig. 2. Mating sites of *A. glomeratus* on cabbage leaves on 29th May. The males from other-clutches showed wing vibrating behaviour ($\triangle$) near the cluster, and the copulation ($\blacktriangle$) also occurred near it. The cabbage plant is sketched by overlooking. ($\bullet$, newly set cocoon cluster. $\circ$, empty cocoon cluster.) 9 : 00–10 : 00, 29th May.

cocoon clusters began wing vibration within 5 cm from a cluster, 12% from 5 to 10 cm and none from more than 10 cm (Table 1). Most of the matings took place near the cluster. Out of 29 successful mating pairs, 16 pairs copulated within 5 cm from the cluster, 12 pairs from 5 to 10 cm and one pair from 10 to 20 cm (Table 1).

The empty cocoon clusters after the emergence of the wasps also attracted males. Table 2A indicates the percentage of empty cocoon clusters which attracted males after the emergence of the wasps. Thirty-three percent (4/12) of the cocoon clusters 4 days after the emergence still attracted males. The ether-washed cocoon clusters, however, did not attract males (Table 2B).

On the other hand, the behaviour of the females was quite different from that of males (Fig. 1). The female wasps after emergence walked a short distance (ca. 5 to 10 cm) straight away from the cluster and stood still. Most of the resting females were often mounted by searching males. If a female was standing still and receptive, copulation took place. After mating, the female flew away. However, if she did not accept the male, she walked or flew a short distance away, or dropped from the leaf.

The length of time of the wasps' stay near the cocoon cluster was investigated, since it was thought to be important to the chances of mating. Table 3 shows the length of time the males stayed within 10 cm of their cluster. Eighty-three (135/162)

Table 1. NUMBER OF MALES SHOWING THE WING VIBRATION RESPONSES AND THE SUCCESSFUL COPULATION AT SOME DISTANCE FROM THE COCOON CLUSTER

Distance from the cluster	0–5 cm	5–10 cm	10–20 cm	20 cm—
No. of males observed			126	
Wing vibration ^a	111 (88.1%)	15 (11.9%)	0	0
No. of mating pairs observed			29	
Copulation	16 (55.2%)	12 (41.4%)	1 (3.4%)	0

^a Responses of same-clutch males are excluded.

Table 2. RELATIONSHIPS BETWEEN THE NUMBER OF EMPTY COCOON CLUSTERS WHICH ATTRACTED THE MALES AND THE DAYS AFTER EMERGENCE OF THE WASPS

Days after emergence of wasps	0	1	2	3	4	5—	
A	No. of empty cocoon clusters examined	cocoons 12 (36.8±13.7		females (25.8±12.0)) ^a			
	No. (%) of empty clusters which attracted males	12 (100)	12 (100)	8 (66.7)	7 (58.3)	4 (33.3)	0
	No. of ether-washed empty cocoon clusters examined	cocoons 10 (39.9±17.2		females (18.1±6.5)) ^a			
B	No. of ether-washed empty cocoon clusters which attracted males	0	0	0	0	0	0

A ; with no treatment. B ; cocoon clusters were washed by ether immediately after emergence of the wasps.

^a mean number ($\bar{x} \pm \text{S.D.}$) of the cocoons and the females involved in a cluster.

Table 3. RELATIONSHIPS BETWEEN THE NUMBER OF MALES STAYING WITHIN 10 cm FROM THE COCOON CLUSTER AND THE TIME AFTER THEIR EMERGENCE

Time after male emergence (in min.)	0	1	3	5
No. of cocoon clusters observed		cocoons 12 (51.8±20.5	females (31.1±13.4)) ^a	
No. of males observed		162		
No. (%) of males stayed	162 (100)	135 (83.3)	117 (72.2)	108 (66.7)

^a mean number ($\bar{x} \pm \text{S.D.}$) of the cocoons and the females involved in a cluster.

Table 4. RELATIONSHIPS BETWEEN THE NUMBER OF THE FEMALES COPULATED AND THE TIME AFTER THEIR EMERGENCE

Time after female emergence (in min.)	0—3	3—5	5—
No. of females observed	63		
No. of females copulated	14	5	0

and 72 (117/162) percent of the males stayed near the cluster for 1 minute and 3 minutes after their emergence, respectively. More than half (108/162) of the males remained near the cluster exhibiting searching behaviour for at least 5 minutes after their emergence. Females would remain still for hours, if they were not disturbed by a male, wind or other factors.

Successful mating was accomplished in a few minutes after the emergence of females: 14 of 19 females whose movement could be traced till their successful copulation were mated in 3 minutes, and 5 of them in 3 to 5 minutes after their emergence (Table 4). No females mated later than 5 minutes from their emergence.

These data suggested that the mating in the field took place near the cocoon cluster immediately after emergence, and that high percentage of sib-matings occurred. In the successful matings, the percentage of inbreeding was 58.6 (17/29).

DISCUSSION

The male wasps emerged earlier than females both in the laboratory and field as had been reported (MATHESON, 1907; KITANO, 1976). They remained on or near the cocoon cluster after emergence and showed antennal movement and wing vibration. Males reaching the cluster from other emerging ones also exhibited wing vibration suggesting the existence of a female sex pheromone in the cocoons. Cocoon clusters after washing with ether and empty ones in the field for several days after wasps' emergence did not elicit a response in males (Table 2B).

The female wasps after emergence walked several cm from their own cluster and stood still. KITANO (1976) suggested that this behaviour reduced inbreeding. Now, we believe it reduces crowding and confusion near the cluster.

It seemed to be important that the clusters were attractive to males. By this, the chances of encounter of two sexes in the field might increase.

Our results suggest that the main site where mating takes place in the field is near clusters where females have newly emerged. The size of the active space of pheromone of a cluster is estimated to be about 10 cm in radius, as all males exhibited wing vibration within this area and most of the mating pairs were observed within 10 cm of the cluster (Table 1).

The pheromone area produced by only one female appears to be smaller than that of the cluster which usually includes some females, and the size of it is thought to be a few cm in radius according to our observations. Females resting within several cm of a cluster were encountered by searching males. When females were quiet and receptive, copulation readily took place, but males in intense activity sometimes drove the females away. The behaviour of the females also appeared to be important in mating.

Fig. 3 schematically indicates the probability of mating with a cohort during time. There are usually a few males from other cocoon clusters present at a cluster just prior to and when emergence is taking place (Mo-males). Males from the cluster

Fig. 3. Change in the number of *A. glomeratus* near the cluster after emergence is schematically drawn. M_s and M_o are the number of same-clutch males and of other-clutch ones, respectively. F is the number of females. The area of oblique lines indicates the number of males that are facing the chances of mating.

begin emerging prior to the emergence of females (Ms-males). As the females begin to emerge, the male population is in favor of cohost males resulting in a high degree of inbreeding. Through time the cohost males begin to disperse, so females emerging later have an increased probability of encounter with a male from another cluster resulting in decreased inbreeding of later emerging females.

It would be expected that cocoon clusters of *A. glomeratus* are distributed more sparsely in nature than in our test field. So, the ratio of Mo to Ms would not be as great as indicated in Figure 3, and the probability of inbreeding would be greater than indicated and probably represents a natural phenomenon.

In *Habrobracon juglandis*, the existence of inbreeding depression has been reported (WHITING, 1925). In *A. glomeratus*, the evidence for the existence of a similar depression has not been reported.

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